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⑦ " anatomy
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Proceedings of the

TENTH INTERNATIONAL CONGRESS OF ENTOMOLOGY

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volume 1

INTRODUCTIONS
SYSTEMATICS
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THE CONGRESS INSECT

The illustration on the cover is *Grylloblatta campodeiformis*, an insect discovered near Banff, Alberta, in 1913, by Dr. E. M. Walker, Emeritus Professor of Zoology at the University of Toronto and an Honorary Vice-President of this Congress. It is, perhaps, from the anatomical or phyletic standpoint, the most remarkable of Canadian insects. In a general sense an orthopteroid, it shows resemblances both to the Saltatoria and to the Blattaria and, together with a more recently discovered Japanese genus, ranks as an independent suborder or order.

Grylloblatta is adapted to cold conditions. It is found in the Rocky Mountains, near the timberline, living in decaying wood or moss among loose rock. It feeds on other insects and is nocturnal in habits.

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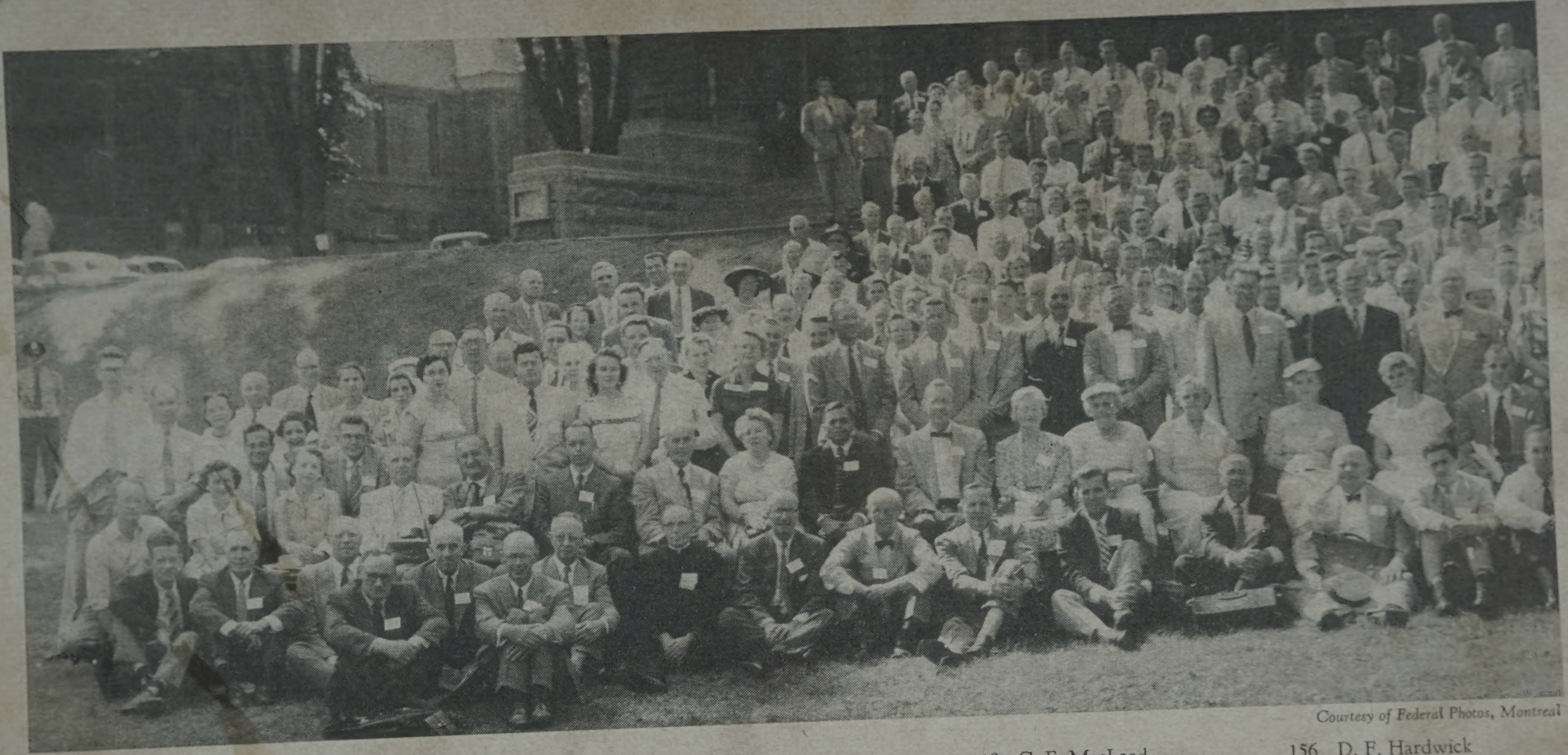

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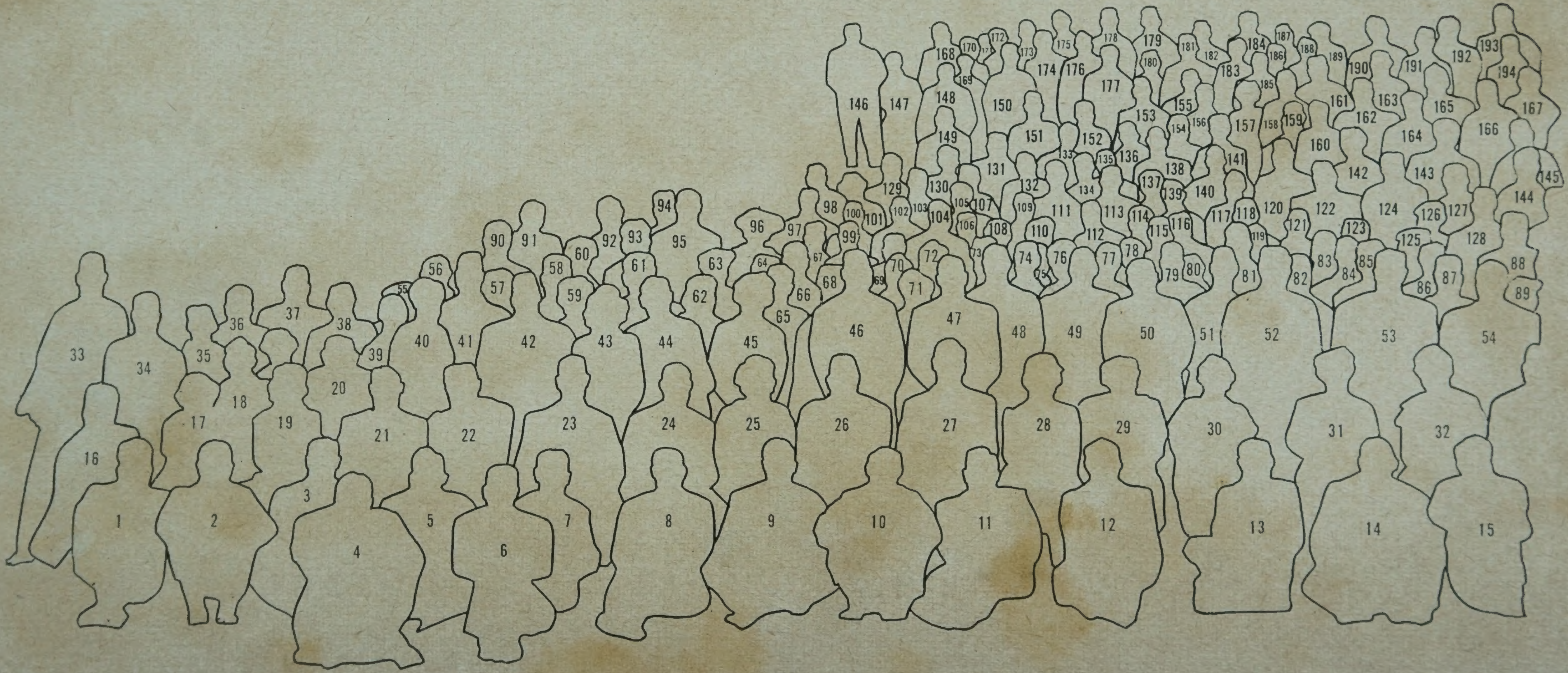
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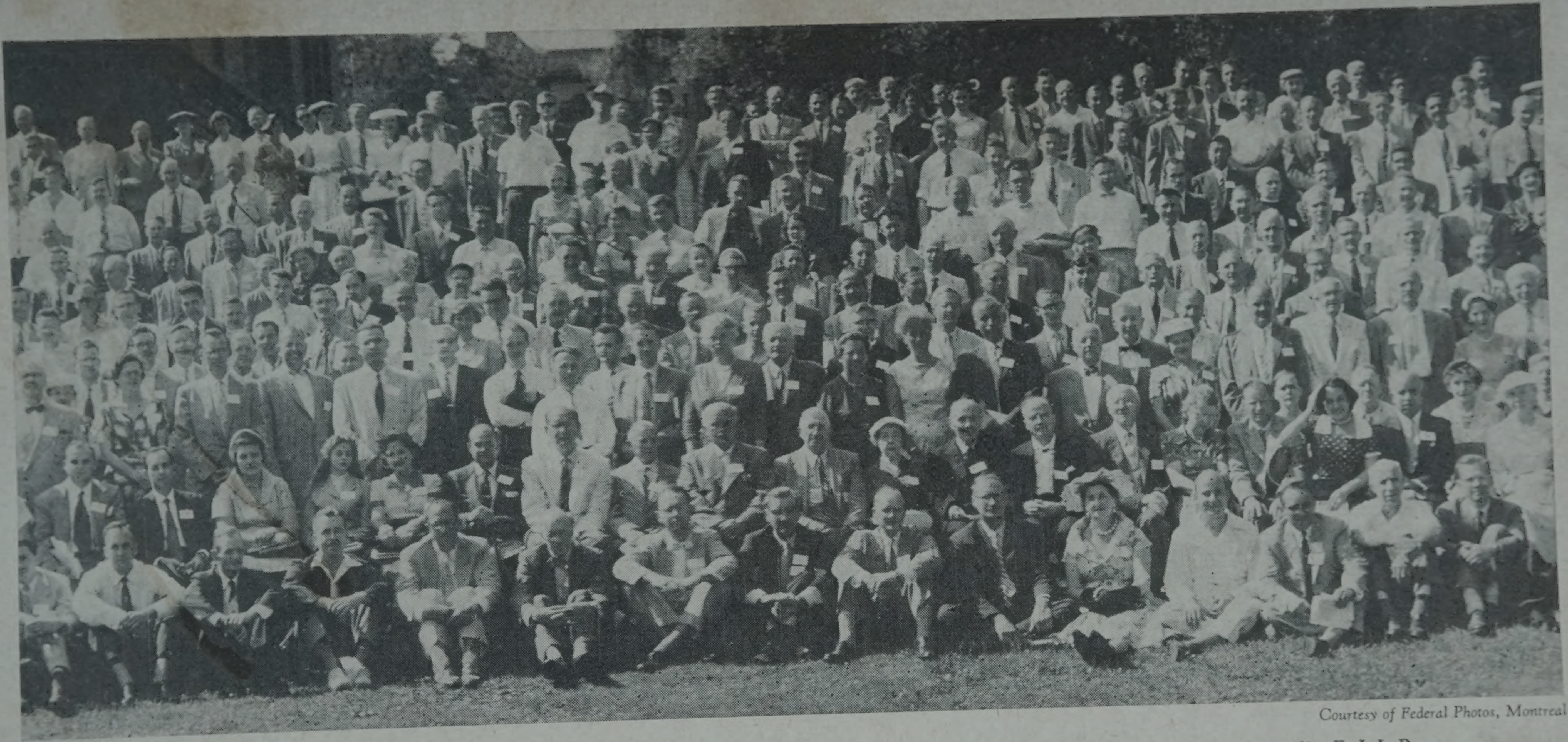

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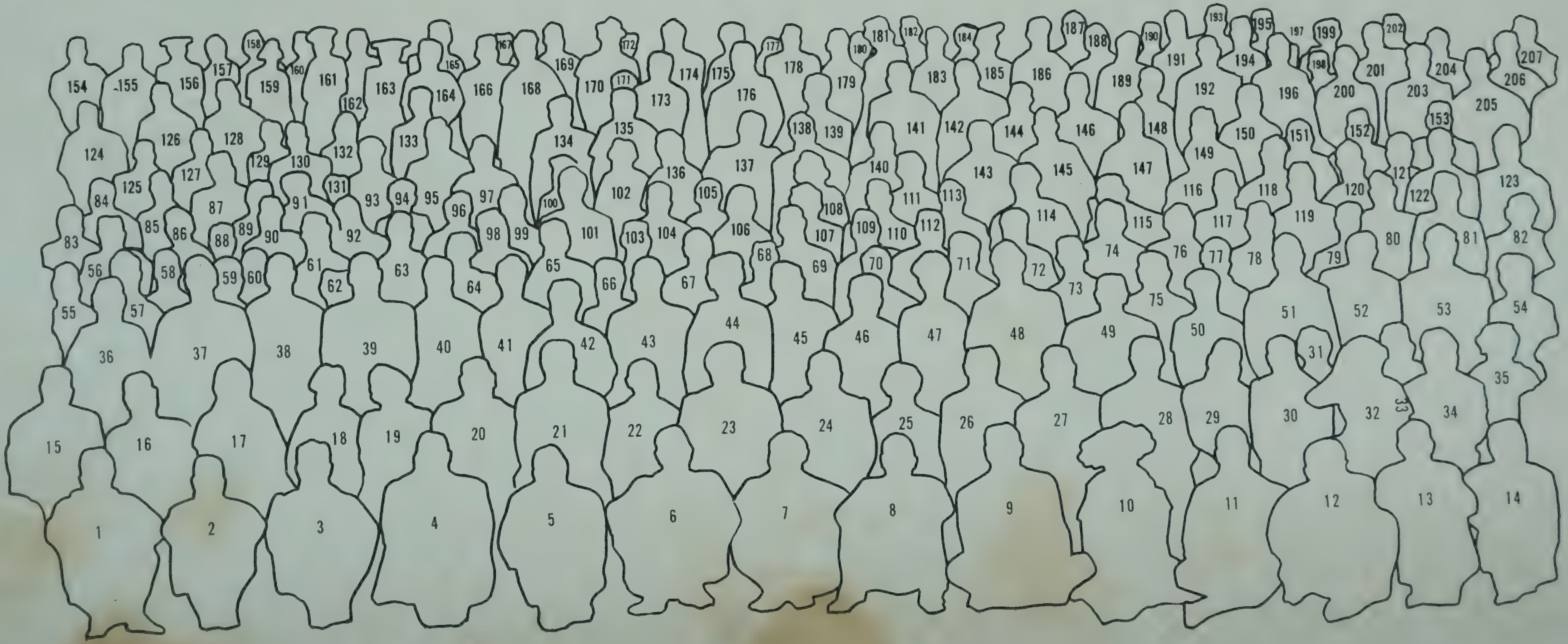
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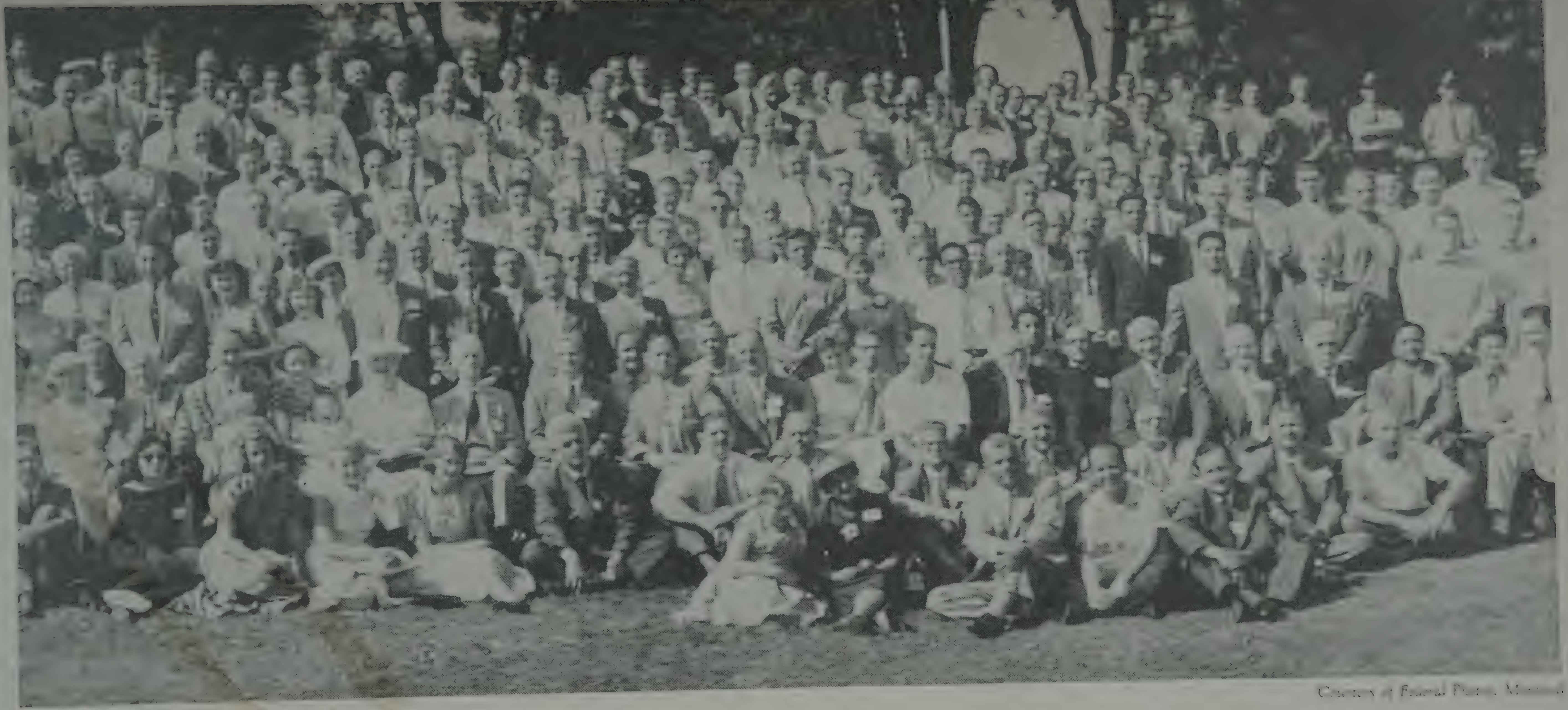

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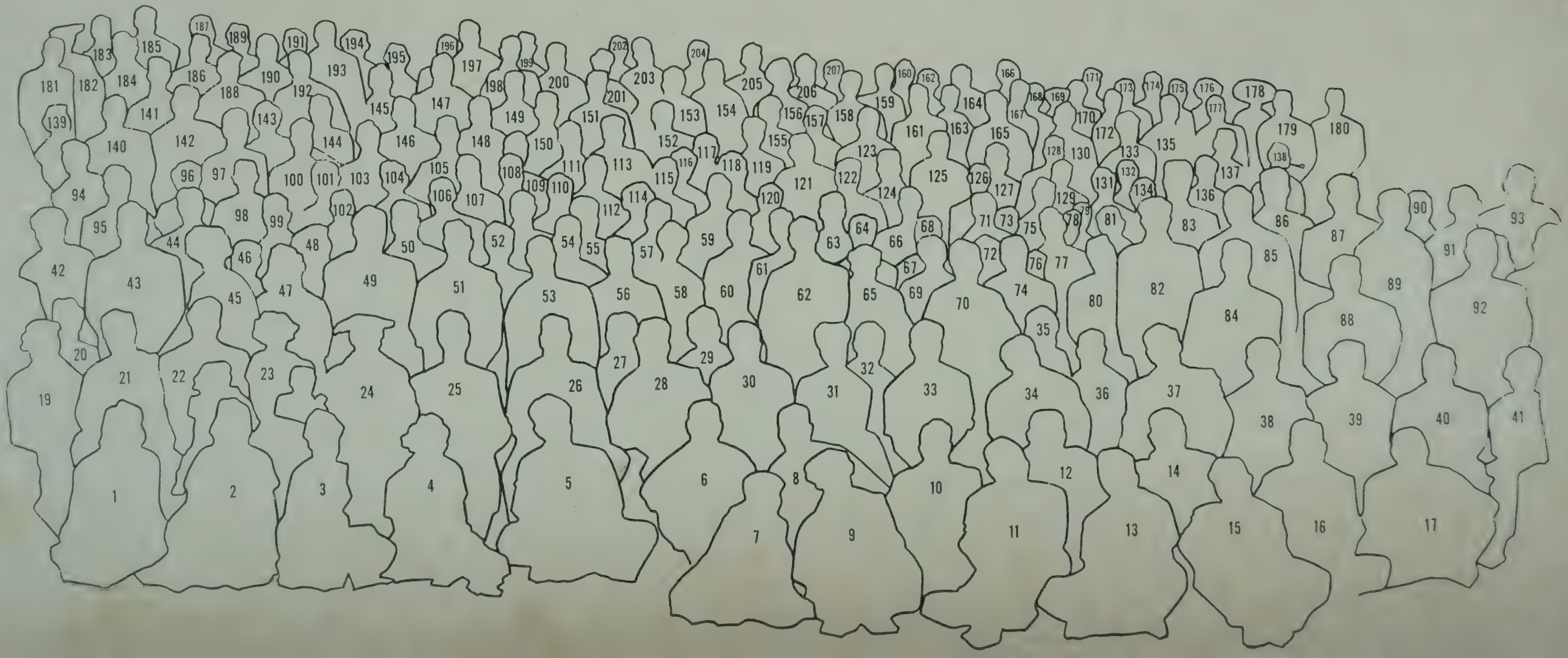
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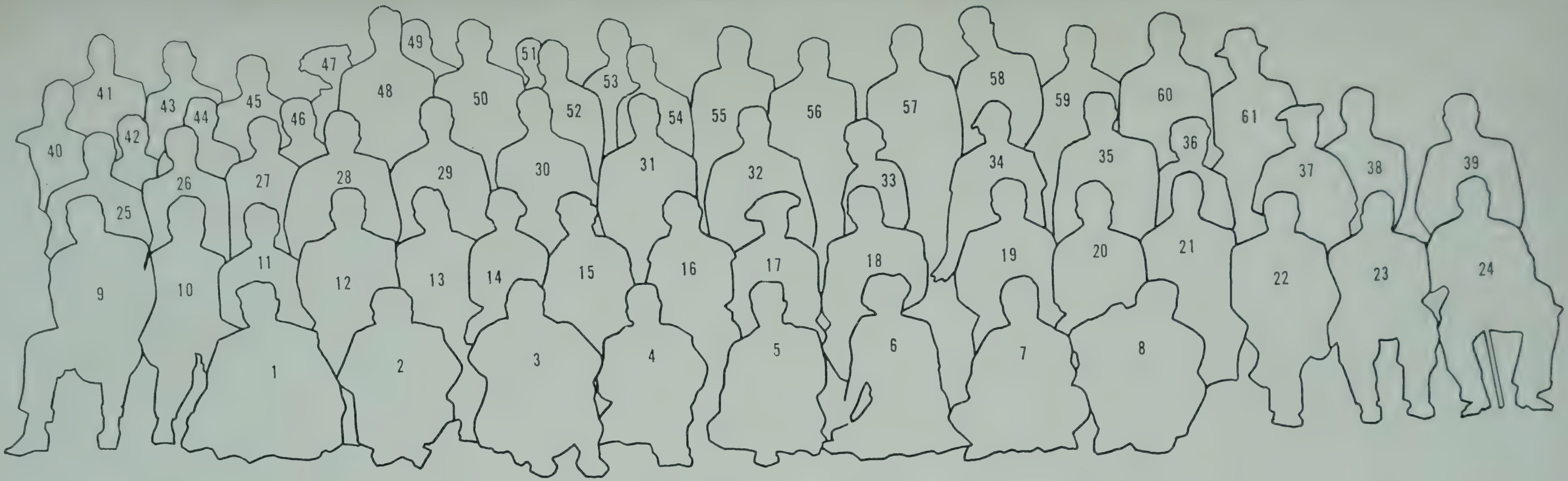

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NOTE: The following members signed the circulated sheets when the photograph was taken; however, all attempts to identify them have failed.

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W. G. Bruce
R. Couture
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Proceedings of the International Congresses of Entomology

First International Congress of Entomology, Bruxelles, 1910. Printer: Hayez, Imprimeur des Académies Royales, Bruxelles.
Volume I. Historique et Procès-verbaux. 276 pp. June 15, 1912.
Volume II. Mémoires. 520 pp., 27 pls. October 30, 1911.

Second International Congress of Entomology, Oxford, 1912. Editors: K. Jordan and H. Eltringham. Printer: Hazell, Watson, & Viney, Ltd., London and Aylesbury.
Volume I. Proceedings. 183 pp., pls. 1–2. February, 1914.
Volume II. Transactions. 489 pp., pls. 3–34. October 6, 1913.

Third International Congress of Entomology, Zürich, 1925. Editors: K. Jordan and W. Horn. Printer: G. Uschmann, Weimar.
Band I. Verhandlungen. 72 pp. August, 1926.
Band II. Verhandlungen. 646 pp., 20 pls. August, 1926.

Fourth International Congress of Entomology, Ithaca, 1928. Editors: K. Jordan and W. Horn. Printer: Gottfr. Pätz, Naumburg A/Saale.
Volume I. Proceedings. viii + 83 pp. March, 1930.
Volume II. Transactions. viii + 1037 pp., 12 pls. December, 1929.

Fifth International Congress of Entomology, Paris, 1932. Editors: L. Berland et R. Jeannel. Printer: Firmin-Didot, Mesnil-sur-l'Estrée.
I. Compte Rendu. 59 pp. 1933.
II. Travaux. 915 pp., 36 pls. December 30, 1933.

Sixth International Congress of Entomology, Madrid, 1935. Printer: S. Aguirre, Madrid.
Tomo I. Pp. 1–406, pls. 1–12. 1940.
Tomo II. Pp. 405–961, pls. 13–38. 1940.

Seventh International Congress of Entomology, Berlin, 1938. Editors: K. Jordan und E. M. Hering. Printer: G. Uschmann, Weimar.
Band I. Verhandlungen. Pp. 1–617, pls. 1–29. April, 1939.
Band II. Verhandlungen. Pp. 618–1424, pls. 30–162. July, 1939.
Band III. Verhandlungen. Pp. 1425–2276, pls. 163–243. August, 1939.
Band IV. Verhandlungen. Pp. 2277–3130, pls. 244–294. December, 1939.
Band V. Kongressbericht. ccxliv pp., 7 pls. February, 1940.

Eighth International Congress of Entomology, Stockholm, 1948. Printer: Axel R. Elfströms, Stockholm.
Proceedings. 1030 pp., illust. 1950.

Ninth International Congress of Entomology, Amsterdam, 1951. Printer: Excelsior's Photo-offset, The Hague.
Volume I. Transactions. lxi + 1115 pp., illust. 1952.
Volume II. Transactions. vii + 361 pp., illust. 1953.

Tenth International Congress of Entomology, Montreal, 1956. Managing Editor: Edward C. Becker. Printer: Mortimer Ltd., Ottawa.
Volume 1. Proceedings. 941 pp., illust. December, 1958.
Volume 2. Proceedings. 1055 pp., illust. December, 1958.
Volume 3. Proceedings. 895 pp., illust. December, 1958.
Volume 4. Proceedings. 1115 pp., illust. December, 1958.

Preface

There were 722 scientific contributions presented or read by title at the Congress; twelve of these were cancelled for one reason or another. Thus, of the 710 papers, it is encouraging that 686 are included in the Proceedings either as complete texts or as abstracts.

The task of editing over 10,000 pages of manuscripts was enormous even when divided among the Section Editors. To accomplish the job with as little disruption to their regular duties as possible and within a reasonable time, the Editorial Committee adopted a liberal editorial policy. The committee also agreed that each Section Editor would be responsible for editing his respective section. Thus, rather than appoint an editor-in-chief, the committee appointed a managing editor whose principal duty was to ensure uniformity. Each Section Editor assumed full responsiblility for his section although in several instances he enlisted the aid of colleagues. At least 25 entomologists assisted in the editing and most of them are listed on the appropriate title page preceding each section. Certain others who edited foreign language papers in more than one section are acknowledged below.

The galley proof of each paper was sent to the author for correcting. Most authors cooperated and returned the proofs within the time allotted; however in a few cases when the proofs were not returned, the Section Editor had to check them for readability. The Section Editors were responsible for the page proofs.

The officers of the bio-Graphic Unit, Science Service, Ottawa, Ont., deserve special thanks for their help in remounting many of the illustrations. In a number of instances they had to re-draw the illustrations to make them legible.

Several foreign language manuscripts were edited by the following: the late Dr. Robert Lambert, Ottawa, Ont.; Mr. L. J. Briand, Belleville, Ont.; and Dr. Jacques L. Auclair, St. Jean, Que., edited several of the French manuscripts. Dr. K. Leius, Belleville, Ont.; and Drs. G. H. Bergold and G. Stehr, Sault Ste. Marie, Ont., edited some of the German manuscripts. Dr. Leius also translated some of the Russian scientific journal names. Dr. D. C. Lloyd, Fontana, Calif., edited all of the Spanish manuscripts and Dr. W. R. Thompson, Ottawa, Ont., edited all of the Italian manuscripts. I wish to thank these entomologists for their help. Thanks are also due to Miss Ruth Hollinsworth for her assistance with many details in the preparation of the Proceedings.

I also wish to thank the Section Editors and their assistants for adhering to the deadlines, and especially the authors who, with very few exceptions, returned their manuscripts on time. Needless to say, without the cooperation of everyone concerned the Proceedings would not have been published so promptly.

Edward C. Becker,
Managing Editor.

Introductory Remarks

At the Plenary Session of the IXth International Congress of Entomology held in Amsterdam, Mr. N. D. Riley, Secretary of the Permanent Committee, informed the Congress that invitations with regard to the next meeting had been received from several sources and he mentioned particularly a most attractive proposal from South America. It was then revealed that this invitation was from the Government of Brazil. However the Committee considered that it required more time to examine the various proposals submitted to it and recommended only to the Congress that the next meeting be held in 1955.

During the following two or three years political developments in Brazil became increasingly unfavourable to the plans of the Brazilian entomologists and at the end of 1954 Professor A. W. Baker, then President of the Entomological Society of Canada, received word from Mr. Riley that Brazil might be unable to hold a congress in 1955 and that an invitation from Canada might be welcomed. After discussing the matter carefully the Directors of the Entomological Society of Canada decided that Professor Baker should let Mr. Riley know that the Society would be prepared to consider inviting the Congress if a meeting in Brazil should actually not be possible but that the meeting would probably have to be postponed until 1956. In October 1954 Professor Baker informed the Directors of the Entomological Society that the majority of the Permanent Committee were in favour of holding the meeting in Canada if possible. The Directors then decided to approach the Government of Canada for a grant sufficient to cover a substantial part of the basic expenses anticipated. In December 1954 a brief was submitted to the Canadian Government explaining the purpose and value of the International Congress and requesting a grant-in-aid. Matters having reached that stage it was considered advisable to create a Congress Committee and this was appointed by the Directors of the Entomological Society of Canada with W. R. Thompson as Chairman, R. Glen and M. L. Prebble as members and J. A. Downes as Secretary. This committee was given power to add to its numbers if a meeting should be held in Canada in 1956. Some anxious months then elapsed while the committee waited on the decision of the Canadian Government and it was not until the end of June that it was possible to report to the Directors of the Entomological Society that the Government had agreed in principle to a grant in support of the Congress. However even before this was known the Executive Committee was rapidly enlarged so that it could cover the mass of urgent work that had to be dealt with before the meeting in the summer of 1956. The first Congress circular was issued in July 1955, the second circular in February 1956 and a preprint of the scientific programme in July 1956. The complete programme of the Congress and a special number of the Canadian Entomologist issued to commemorate the occasion and containing a brief history of the International Congresses, a review of entomology in Canada up to 1956, and a study of Canada as an environment for insect life were completed for distribution together with many circulars and brochures, containing additional information, in advance of the opening of the Congress on August 17th.

Much careful thought was given to the choice of a site for the Congress. It was clear that in a country like Canada with its vast size and relatively small population it would not be easy to select a locality easily accessible to European visitors and presenting the features of the great centres in which most of the Congresses of the past have been held. Eventually it was decided to hold the Congress in Montreal which is the largest and most cosmopolitan of Canadian cities and the site of two of its oldest universities, one English speaking the other French speaking—McGill University and the Université de Montréal—and one of the principal ports of Eastern North America for trans-atlantic vessels and aircraft. The choice of Montreal was certainly justified by the event, since the Congress was the largest that has ever assembled and it would probably have been difficult to find accommodation for its members in any other Canadian city.

One of the major problems that confronts the organizers of scientific congresses is the financial problem. This was particularly acute in connection with the Xth Congress because to make it successful its international character had to be maintained and yet the cost of attending a Congress in Canada was, for many entomologists from outside North America, much too great to be met from their private resources. The entomologists of Canada wished also to give as many delegates as possible an opportunity to see something of Canada, to inspect entomological work in progress and to utilize the unequalled opportunity for an exchange of views on their problems. The sum of about $30,000.00 was distributed from Congress funds to delegates from all parts of the world for these purposes.

The attendance at the Congress was most gratifying as there were 1,459 (including 403 associates) members who came to the meetings in Montreal. They represented 57 countries including 641 from the United States, 537 from Canada, 212 from Eurasia, 42 from Central and South America, 20 from Africa, and 7 from the Australian region. The total membership (including the 175 who could not attend) was 1,634 representing 67 countries.

The writer feels sure that those who attended the Congress would wish its President to acknowledge and thank in their name all those who contributed to its success. McGill University, the Université de Montréal and the Protestant School Board of Montreal most generously placed their buildings and facilities at the disposal of the Congress, the Federal Government, a number of Provincial Governments, universities and colleges, Entomological Societies and other associations as well as a very large number of industrial and commercial organizations and private individuals responded generously to appeals for financial assistance. A complete list of the various bodies to which the Congress is indebted in various ways was printed in the Programme.

It is also a pleasure to acknowledge the devoted and untiring labours of the members of the Executive Committee and the many other committees who carried out the difficult work of planning and organization. The Secretary, his associates and assistants deserve very special mention but it must be stressed that the organization of the Xth Congress was in a very special sense a collective effort in which a great number of Canadian entomologists wholeheartedly shared. Finally it must be said that without the special arrangements made by the Federal Divisions of Entomology and Forest Biology and the two Universities in Montreal the assistance of their staffs would not have been available.

W. R. Thompson,
President, Tenth International
Congress of Entomology.

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Proceedings

The following account of the Proceedings of the Congress touches only on the most important events. For a detailed day by day account and a statement of the facilities provided, organizers of future congresses and others interested are advised to consult the official programme.

The Congress headquarters in the Montreal High School were opened for registration and the supply of information on August 16th and remained opened until August 25th when the Congress ended, though the information centre was maintained until the evening of August 19th. The Scientific meetings were held at McGill University from Friday, August 17th to Monday, August 20th and at the Université de Montréal from Wednesday, August 22nd to Saturday, August 25th. A small staff was moved to the Université de Montréal to maintain liaison with the head offices in the Montreal High School.

On Friday August 17th the Congress was officially opened by the President at a Plenary session held on the East Campus of McGill University. On the platform were a number of members of the Honorary Committee and of the Permanent Committee of the International Congresses and the principal Congress officers. The President's opening address was as follows:

Ladies and Gentlemen:

It is my great honour and privilege, in the name of the Entomological Society of Canada, to open this Tenth International Congress of Entomology: the second to be held on this continent and the first to be held in Canada; and to welcome on behalf of the entomologists of Canada this splendid gathering of colleagues and friends from so many parts of the world. We realize that for many of those attending the Congress the selection of Canada for the meeting has created special difficulties. We have tried to alleviate these difficulties. In fact the sum of approximately $30,000.00 has been distributed by the Executive Committee in assisting overseas entomologists to come to the Congress and to travel inside Canada. I should stress the fact that this money was very hard to get and was obtained only by the most strenuous efforts by many members of the Executive Committee. We know of course that the financial help we have been able to give has not always been adequate and that many of those attending the Congress have had to make a personal sacrifice in order to do so. They also will have contributed very definitely to the success of the Congress.

As you know, His Excellency the Governor General of Canada has graciously consented to act as Patron of the Congress and although it was impossible for him to attend he has wished to show his interest in our proceedings by a message which I will now read: (I SHOULD LIKE TO SEND MY WARMEST GOOD WISHES TO ALL THOSE ATTENDING THE TENTH INTERNATIONAL CONGRESS OF ENTOMOLOGY NOW BEING HELD IN MONTREAL AND TO WISH YOU ALL SUCCESS AND GOOD FORTUNE IN YOUR DELIBERATIONS. SIGNED VINCENT MASSEY).

I am sure you will all wish me to convey to His Excellency our warm appreciation of this token of his interest in our meetings and in the science of entomology.

We are much gratified to have with us today a number of the distinguished members of our Honorary Committee. They represent Government Departments, Universities, Civic Administration and Industrial Organizations which by their financial contributions and their hospitality and also by the technical help they have placed at our disposal have made the holding of the Congress possible. You have the names of these distinguished gentlemen in the printed programme and I hope you will have the opportunity of meeting some of them after this meeting. I should add that the Right Hon. Mr. Gardiner is represented by Senator Godbout, His Worship, Mr. Jean Drapeau, Mayor of Montreal, by Dr. Albert Guilbeault, Pro-Mayor, and Dr. Taggart, Deputy Minister of Agriculture in the Federal Government, by Mr. S. J. Chagnon, Assistant Deputy Minister. The Hon. Mr. Barré, Dr. Neatby and Mr. Fowler have been unable to attend.

Messieurs les membres du Comité d'Honneur; Messieurs et Dames:

Avec cette séance nous venons de lancer le dixième congrès international d'entomologie, honoré par le patronage de Son Excellence le Gouverneur-Général qui nous a gracieusement envoyé le message que je vous ai lu tout à l'heure.

Comme vous le savez, le congrès de 1928 s'est réuni aux Etats-Unis; mais le congrès de '56 est le premier congrès spécifiquement canadien. Cédant aux instances désespérées du Comité Permanent, nous avons finalement consenti d'organiser cette manifestation, dont la réussite nous paraissait pendant longtemps plutôt problématique. Ce sera à vous, chers Collègues, de nous dire, pas maintenant, certes, mais après le congrès, si nous avons été à la hauteur de notre tâche.

Nous avons discuté pendant pendant assez longtemps, le local du congrès. Finalement nous nous sommes décidés pour Montréal. Montréal est la plus grande ville du Canada; notre plus grand port maritime et aérien, présentant donc des facilités spéciales pour la plupart des délégués d'outre-mer. Aussi et surtout c'est une ville bilingue et pleine de souvenirs historiques, chers à tous nous autres Canadiens où les deux grandes races qui ont fondé notre pays vivent harmonieusement ensemble. Elle a deux grandes Universités: McGill, Université où vous vous trouvez présentement, et qui est surtout une université de langue anglaise, et l'Université de Montréal, où nous allons déménager la semaine prochaine et qui est surtout une université de langue française; chacune, cependant, à sa manière, un centre de la haute culture canadienne.

Comme je l'ai déjà dit, nous sommes heureux d'avoir avec nous aujourd'hui, des membres de notre comité d'honneur. Comme vous le savez, ce sont des personnages distingués qui ont bien voulu s'associer à notre effort et c'est surtout grâce aux subventions et à l'hospitalité accordées par leur intervention que nous avons pu résoudre un de nos plus angoissants problèmes: le problème financier. Vous avez certainement trouvé les noms de ces messieurs dans le programme et vous aurez sans doute l'occasion de les voir de plus près à la fin de la séance.

The representatives of the Federal Government of Canada of the Government of the Province of Quebec, of the city of Montreal and of the two host Universities, McGill University and the University of Montreal have kindly consented to welcome the members of the Congress on behalf of their respective administrations and institutions. I will therefore call on Senator Godbout, the Honorable Mr. Bourque, Minister of Lands and Forest of the Province of Quebec, Dr. Guilbeault representing the Mayor of the City of Montreal, Dr. Cyril James, Principal of McGill University and Monsignor Irenée Lussier, Rector of the University of Montreal, to speak to the Congress.

The addresses of the members of the Honorary Committee, with the exception of Senator Godbout whose very regrettable death from an accident occurred not long after the Congress, were as follows:

Hon. Mr. Bourque:

Messieurs, Mesdames:

Il me fait plaisir au nom du gouvernement de la Province de Québec de vous souhaiter la plus cordiale bienvenue à ce Dixième Congrès International d'Entomologie.

Veuillez croire que nous sommes grandement honorés du fait que vous avez choisi la Province de Québec et la Cité de Montréal, en particulier, pour la tenue de votre Congrès. Il n'y a pas de doute que vous avez voulu, de cette façon, mettre une fois de plus en évidence le caractère bi-ethnique de notre population, et en même temps, rendre hommage au dévouement et à la science de nos entomologistes.

Dans une province comme la nôtre, où l'agriculture et la forêt assurent le bien-être de la population, la lutte contre les insectes nuisibles s'impose. Les pertes causées à nos forêts par les epidémies d'insectes ont suscité l'attention des autorités gouvernementales qui ne veulent négliger aucun moyen pour en assurer la protection et la conservation. C'est pourquoi nous espérons que la réunion d'un si grand nombre d'entomologistes distingués venus de tous les coins du globe, apportera une contribution efficace à la lutte contre ce fléau.

L'on se rend compte, de plus en plus, du rôle de la science dans l'économie moderne. L'on reconnaît, en effet, qu'il est absolument nécessaire d'exploiter nos ressources naturelles selon les données scientifiques les mieux appropriées aux circonstances. Voilà pourquoi le gouvernement de cette province a été heureux de contribuer à l'organisation matérielle de ce Congrès pour le plus grand bienfait de sa population et de l'humanité tout entière. Mes meilleurs voeux de succès vous accompagnent.

DR. GUILBEAULT:

Monsieur le président, mesdames et messieurs:

Nous apprécions très hautement votre venue à Montréal.

Je sais que ce n'est pas la beauté de notre ville en pleine évolution qui vous a guidés ici. Plusieurs autres villes du continent américain méritent votre admiration.

Depuis 25 ans notre ville a doublé sa population. Toutes les activités de l'esprit humain sont à prendre leur essor. Les travaux des entomologistes canadiens ont peut-être attiré votre attention. Nous en sommes fiers. La tenue du 10e congrès international d'Entomologie sera un encouragement précieux pour nos savants.

Il est un fait constant que la présence dans un pays des plus grands savants du monde constitue une semence de curiosité scientifique, de nouvelles méthodes d'investigations qui se traduit dans les années à venir par une production scientifique accrue.

Peut-être aussi avez-vous désiré vivre la vie canadienne pendant quelques jours; la vie de la métropole du Canada et de la deuxième ville de langue française du monde. Ce titre est cher au coeur des Montréalais dont 70% sont de langue et d'origine françaises.

Il est vrai que ces origines sont lointaines et remontent à deux ou trois siècles. Mais pour nous Canadiens de langue française le doux nom de France évoque toujours: beauté, intelligence, et amour: amour de la vérité, amour de la clarté, amour de l'humanité.

C'est grâce à ces qualités héritées de nos ancêtres que nous vivons heureux dans ce Canada qui est bien nôtre tout comme il appartient aussi à nos concitoyens de langue anglaise.

Unis sous la même couronne, fidèles à la même reine, tous les canadiens veulent un Canada de plus en plus grand, de plus en plus beau. C'est pourquoi la ville de Montréal est particulièrement heureuse aujourd'hui d'être pour une semaine devenue le centre du monde pour les entomologistes.

C'est de tout coeur, Monsieur le président, mesdames et messieurs, que la Ville de Montréal, par mon humble voix, vous souhaite la bienvenue.

Puisse vos travaux continuer à contribuer d'une manière toujours éclatante au bien-être et au bonheur de l'humanité.

DR. JAMES:

Mr. President, Ladies and Gentlemen:

It is a privilege, this afternoon, to endorse the sentiments that have already been so splendidly expressed and to bid you welcome to McGill University.

Those who have spoken before me have underlined the economic significance of entomological research for Canada. Farms and forests are important to Canada: the spruce budworm may become as significant in our history as the boll weevil was for the United States. We are delighted that you, delegates from distant countries, have come to share your knowledge with us and to study our problems.

This campus, this tree-shaded lawn, on which we are gathered this afternoon, is perhaps the most appropriate place in all of North America for an international meeting. More than four hundred years ago, when Jacques Cartier sailed up the St. Lawrence in search of China (the town of La Chine, ironically named, is only a few miles west of here!), he was stopped not far from here by the rapids. This spot marks the end of his voyage and here, by the Indian settlement of Hochelaga, Cartier held his great meeting with the Indian chiefs at which he explained the glory of France and, for spiritual edification, read a portion of the Gospel according to St. John.

I have always been a little worried about the problem of communication at that meeting in 1541. I doubt if either party understood the other's intent. But even if there was no immediate meeting of minds, there can be no doubt of the lasting significance of the conference of Hochelaga. Much of the history of North America springs from it—including that Quebec Act that was one of the causes of the American War of Independence. I hope that your meetings of this Tenth International Congress of Entomology may be as fruitful!

You will find here, I hope, not only the memory of historic occasions but the tradition of quiet study and friendly questing. For nearly one hundred and fifty years, McGill University has grown under the shadow of that great elm tree on the acres of what, at the beginning of the nineteenth century, was James McGill's farm. I bid you welcome to the great company of all those who have lived and worked here, for the betterment of mankind, and hope that each of you may find your sojourn pleasant as well as profitable.

MGR. LUSSIER:

Monsieur le Président, Chers congressistes:

Le Recteur de l'Université de Montréal est heureux de pouvoir venir jusqu'à vous pour vous dire, conjointement avec son honorable collègue le Principal de McGill: vous êtes le plus cordialement bienvenus en notre ville et en nos murs. Soyez assurés dès maintenant de trouver l'accueil le plus bienveillant que vous puissiez désirer lorsque vous viendrez chez-nous sur l'autre versant du Mont-Royal, dans quelques jours; du moins nous le voulons ainsi.

Il est devenu coutume que les grands congrès à caractère scientifique et culturel qui se tiennent en notre ville partagent entre nos deux institutions, l'Université McGill de langue anglaise et l'Université de Montréal de langue française, la somme de leurs séances d'études. Cette coutume, de même que le mot de bienvenue que je vous adresse en langue française, est un indice précis du caractère bilingue de notre grande ville: Montréal, la deuxième ville française au monde par la langue de la majorité de sa population, est la métropole du Canada, grand pays du Commonwealth britannique.

Deux races vivent ici côte à côte dans une harmonie comparable à celle qui existe dans la meilleure famille, entre des époux bien unis; cette formule est un indice assez clair de la nécessité d'explications amicales de temps à autre.

Nous sommes orgueilleux de notre co-existence pacifique et nous croyons que dans les temps que nous vivons, nous pouvons servir de modèle en ce point à bien des populations.

Nous attendons beaucoup de vos rencontres, beaucoup sur le plan humain, beaucoup sur le plan international grâce aux amitiés qui vont se lier, beaucoup naturellement, sur le plan scientifique.

Les hommes vont apprendre ici, par vous, à mieux vivre entre eux et à mieux connaître la nature qu'ils habitent; vous allez proclamer qu'il est souvent préférable de souffrir nombre de petits inconvénients dus à la présence d'autres vivants que de risquer de graves déséquilibres en supprimant ces êtres vivants. Votre science vous rend ouverts à toutes les hypothèses charitables; vous commencez par prêter aux êtres apparemment les plus détestables une fin peut-être utile à l'homme et bienfaisante pour lui. Puisse un tel état d'esprit se répandre dans tous les domaines. Si les hommes en arrivaient à voir qu'ils ont en réserve les uns pour les autres des trésors d'utilité, même de bonté, ils se regarderaient avec plus de bienveillance et leur co-habitation serait marquée de moins d'impatience et de moins de querelles.

Mes connaissances en votre domaine sont liées aux Souvenirs Entomologiques de Fabre, livres que j'ai bien aimés durant ma jeunesse. Paraît-il, du moins aux dires de certains d'entre vous, que Fabre a mêlé quelque peu d'imagination à ses observations. Mes seules lectures de Fabre ne me donnent évidemment aucun titre à siéger parmi vous! Mais, heureusement, vous rencontrerez chez-nous des collègues qui ont dépassé les Souvenirs Entomologiques, qui ont apporté leurs contributions personnelles aux progrès de votre science. Je suis heureux de vous inviter dès maintenant à visiter quand vous serez chez-nous l'exposition des travaux d'un observateur de grand mérite le frère Ouellet; resté dans l'ombre en raison de sa vie religieuse, il nous donne aujourd'hui la joie d'admirer la productivité de son silence et sa passion pour le travail scientifique.

Grands succès et à bientôt chez-nous.

After thanking the speakers, the President continued his inaugural remarks as follows:

Messieurs et Dames:

Quarante cinq ans ont séparé le premier et le dixième congrès d'entomologie—dont le rhythme paisible a été brisé par deux terribles guerres. Si l'idée des congrès a persisté c'est grâce surtout à la volonté tenace de l'initiateur de ces manifestations, le vénérable et très respecté Karl Jordan. En raison de son âge avancé il a été impossible pour le Dr Jordan d'assister à notre réunion; mais nous l'avons persuadé de nous dicter un message que vous allez entendre toute à l'heure.

We have now a feature of the programme I am sure you will all welcome: a spoken message from the revered and distinguished entomologist to whose initiative we owe the International Congresses of Entomology: Dr. Karl Jordan, unable himself because of advancing years to attend the meetings. I should add that this is the first of the ten congresses Dr. Jordan has missed. He attended the Congress in Amsterdam although he was then ninety years of age.

As I said a moment ago the idea of the International Congresses of Entomology was due to the initiative of Dr. Jordan. Not long ago there was found in the files of the Division of Entomology in Ottawa the original letter written by Dr. Jordan to Dr. James Fletcher, the first Dominion Entomologist, to enlist his help in the organizing of the congresses. With your permission I will read this letter representing the beginning of an effort that has continued for almost half a century.

> March 9, 1907: Dear Sir:
>
> For the last six months we have been in correspondence with practically all the more prominent European Entomologists about a proposition which we should like to see realized, and I am now writing to solicit also your opinion. Those whom we have consulted almost unanimously agree that it would be very desirable to have an International Association of Entomologists for the advancement of our science, and to organize from time to time an International Congress of Entomologists the first to meet in 1908.
>
> It is hardly necessary for me to point out the beneficent influence such an organization might exercise on Entomology in general, if the organization has the support of all earnest workers. At the Congress, where nobody's attention would be averted by other interests, general questions bearing on entomology might be discussed and thereby the efforts of collectors be guided into channels where their labours are most needed.
>
> The details of the organization will be worked out by a committee.
>
> We should be very pleased if you were in favour of the general idea of the organization. It is desirable, for various reasons, to treat the matter as confidential till a committee has drawn up a report. Yours sincerely, Karl Jordan.

I have only to add that in addition to the message of greetings sent us by Dr. Jordan he has provided a short paper containing some interesting scientific material which will be held over for the Plenary Session. I will now switch you over, as the broadcasters say, to Dr. Jordan.

Mr. President:

When my friend, Norman Riley, informed me that the Tenth International Congress of Entomology would meet in Canada, the prospect of visiting your country attracted me very much, for I had had only a glimpse of it in 1928 when members of the Fourth Entomological Congress went to see the Niagara Falls. However, my endocrines, the guardian angels which look after the proper functioning of the processes of life, soon left me in no doubt that owing to the wear and tear of the many past years, the old body would not be able to produce the energy necessary for attending the Congress. Then you, dear President, and your Organizing Committee came to the rescue by inviting me to address this Opening Meeting by means of a tape recorder. I thank you for the deepest recesses of my soul for thus making me an active member of the Tenth Congress.

I am sure that the Congress will join with me in sending its warm thanks to Dr. Jordan for his message and its best wishes for many continuing years of happy and active life.

No doubt you know that the intervals between congresses are bridged by the activities of a special group of members known as the Permanent Committee. I should like to introduce them also. They are in the second row. From my right to my left you see Professor Tuxen of Denmark, Dr. Kuenen of The Netherlands, (President of the last Congress), Mr. N. D. Riley (Permanent Secretary) on whom we have often had to call for advice, Dr. Hering of Germany, Dr. Handschin of Switzerland, Dr. Ghesquière of Belgium and Dr. J. Chester Bradley of the United States. More than half the members of the Permanent Committee as you will see from the list in the programme have been able to attend our meeting.

As you are aware, we shall have, after thus opening meeting, the Congress photograph, followed by a Garden Party generously provided by McGill University. However, before we disperse, I should like to make known to you some members of the Congress management—the Canadian Executive Committee. You will frequently have occasion to consult them so you should be able to recognize them. Furthermore if the Congress is a success, as we hope it will be, this is due to the whole-hearted efforts they have made and their careful and intelligent planning. I ask the officers to rise when their names are mentioned.

La séance d'ouverture tire vers sa fin: elle sera suivie par la photographie des membres et la fête de jardin offerte par l'Université McGill. Mais avant de fermer la séance, je désire vous présenter quelques membres du comité exécutif que vous aurez souvent l'occasion de consulter et qu'il vous sera donc avantageux de pouvoir reconnaître.

First I must introduce the Abbé Ovila Fournier, retiring President of the Entomological Society of Canada. Father Fournier has always been keenly interested in the development of Canadian entomology, and has given us invaluable assistance in many ways.

Next I will call on Dr. Robert Glen, President of the Entomological Society of Canada and Chief of the great national Division of Entomology. Dr. Glen's wise and well-balanced decisions have, times without number, kept the Congress management on an even keel and is no exaggeration to say that he has supplied the bulk of the man power required by the Executive Committee.

Mr. Alfred Baird, for many years Treasurer of the Entomological Society of Canada, has carried the vitally important and laborious duties of Treasurer of the Congress and with him has been associated Mr. W. N. Keenan, Chief of the Plant Protection Division, in the drive for funds, which owing to their untiring energy, has been successful beyond our expectations.

However, in the work of organization, the most important role has, without doubt, been that of the Secretariat and here I wish to refer quite particularly to the Secretary, Mr. Antony Downes, who working against time and under difficult circumstances, collected and organized over a period of months a team of able helpers. The secretaries of societies and organizations, as we know, are persons who usually do most of the work and get the least credit. I therefore take this opportunity to say that the organising ability and scientific knowledge of Mr. Downes are largely responsible for what has been accomplished. The detailed planning of the proceedings, an immensely detailed and laborious task, has been no less ably handled by Dr. W. G. Friend, Dr. H. Hurtig and Mr. Frank McAlpine. The heavy work of Registration has been carried by Mr. Guy Shewell and though he might prefer to avoid recognition because of the problems it will bring to his door I am afraid this cannot be helped. Finally, I should introduce the Chairmen of the several important working Committees: Mr. G. P. Holland, Chairman of the Programme Committee, Mr. H. L. Seamans, Chairman of the Excursions Committee, and finally Professor and Mrs. John Stanley who have directed the operations of the Montreal Committee and the Ladies Committee; without their help it would have been impossible for the Secretariat, necessarily located in Ottawa, to work out satisfactory arrangements in Montreal. We are most deeply indebted to them. I refrain from mentioning other helpers though there are many who deserve the highest praise, because we must now pass on to the next items in the programme: the Congress photographs and the Garden Party provided for us by McGill University.

The opening session is now closed. Thank you. Merci.

Following the opening session the members of the Congress assembled for the Congress photograph, after which they attended a Garden Party given by McGill University. In the evening of the same day, by courtesy of the Air Officer Commanding Training Command Headquarters, the Royal Canadian Air Force, The Royal Canadian Air Force Training Band gave a concert on the East Campus of McGill University.

On Saturday, August 18, the scientific sessions opened in McGill University. On the evening of that day a large group of the members left on an excursion to Quebec City where they were entertained to lunch by the Government of the Province of Quebec and taken on a tour of the city.

On Tuesday, August 21, an excursion to Ottawa was arranged for the whole Congress. This included tours through the establishments of the National Research Council, the Dominion Experimental Farm, and Science Service; where a display of Canadian insects, art work and other interesting material had been arranged. The delegates visiting the National Research Council were entertained to lunch and were welcomed at the Experimental Farm by Dr. J. G. Taggart, Deputy Minister of Agriculture in the Federal Government, and Mr. S. J. Chagnon, Assistant Deputy Minister.

On Wednesday, August 22 the plenary scientific session, presided over by the Rev. O. Fournier, one of the Vice-Presidents of the Congress was held in the Auditorium of the Université de Montréal. Addresses were given by the President on "The Interpretation of Taxonomy" (see p. 61) by Prof. O. W. Richards of the University of London on "The Content of the Science of Ecology" (see p. 85) and by Dr. Pierre Maillet of the University of Paris on "Le Phylloxéra de la Vigne. Quelques Faits biologiques et les Problèmes qu'ils Soulèvent" (see p. 75). The delegates also had the pleasure of hearing a tape-recording of the scientific address by Dr. Jordan (see p. 59). On the evening of the same day the Congress was entertained to a Buffet Supper at the Chalet in Mount Royal Park, by the Municipality of Montreal. Dr. A. Guilbeault attended as representative of His Worship the Mayor of Montreal, accompanied by Mme Guilbeault.

On Thursday, August 23, the banquet of the Congress made possible by a generous donation from the Canadian Pulp and Paper Association was held in the Windsor Hotel. A number of members of the Honorary Committee attended and discourses were given by Prof. P.-P. Grassé, of the University of Paris; Dr. R. Glen, Vice-President of the Congress, and Mr. R. M. Fowler, President of the Canadian Pulp and Paper Association, as follows

PROF. GRASSÉ:

Messieurs les Présidents, Mesdames, Messieurs,

Bien que le Xe Congrès international d'Entomologie ne soit pas achevé, on peut affirmer qu'il a connu le succès tant par le nombre élevé de ses participants que par la qualité, la nouveauté des communications qui y ont été faites. Mais on serait bien injuste si on n'attribuait pas à ses organisateurs, nos amis Canadiens, la large part qui leur revient dans la réussite d'une vaste entreprise, difficile à conduire et à mener à bien.

Notre gratitude, Messieurs les Organisateurs, va à chacun de vous, car tous vous vous êtes dépensés sans compter, sans ménager votre peine ni votre temps. Nous remercions aussi le Gouvernement fédéral, les Gouvernements provinciaux, les Universités et les Municipalités des villes de Montréal et de Québec ainsi que tous ceux qui par leur générosité, ont facilité notre séjour au Canada et l'ont rendu attrayant.

Au cours de ce Congrès, notre savoir s'est enrichi. L'entomologie nous a paru avoir accompli ses plus grands progrès dans les domaines de l'endocrinologie, de la génétique, de l'écologie et du comportement. Mais nous risquons d'être injuste dans notre appréciation car nous n'avons naturellement pu assister qu'à un nombre restreint de séances scientifiques. Du Congrès d'Amsterdam à celui de Montréal, les gains réalisés sont considérables; la marche de la Science s'accélère prodigieusement. L'entomologie peut être fière de la place de plus en plus large qu'elle tient dans la biologie et la technologie.

Nous avons noué, au cours de ce Congrès, des relations avec plusieurs Collègues étrangers, dont sans doute nous avions déjà lu les travaux, mais la connaissance directe des hommes est plus enrichissante que la seule lecture des oeuvres. Il est regrettable que, trop souvent, des barrières linguistiques s'opposent à des discussions approfondies entre congressistes intéressés aux mêmes problèmes. C'est à lever cette difficulté majeure que les organisateurs des futurs congrès s'employeront sans nul doute. Dans l'état actuel de la planète, aucune langue parlée par un groupe de nations ne peut être imposée au reste de la terre. Toute tentative d'hégémonie linguistique serait actuellement tenue pour vexatoire et serait vouée à l'échec. Il faut pourtant améliorer les échanges intellectuels entre les hommes de science. Au cours des Congrès, la chose n'est point trop difficile, il suffirait de recourir plus largement aux traducteurs. Notre conviction personnelle est qu'on devra, tôt ou tard, adopter pour la rédaction des mémoires scientifiques une langue créée de toutes pièces, au vocabulaire riche et précis, aux règles simples et logiques. Une telle pratique stimulerait puissamment le progrès de la Science, en facilitant la diffusion des nouvelles connaissances. Trop souvent, l'Ouest ignore ce que fait l'Est et inversement. Un tel état de chose ne peut durer encore longtemps. Les Congrès internationaux devraient faciliter son règlement, comme ils devraient servir, plus puissamment qu'ils ne le font, à la diffusion des revues et des livres scientifiques.

Si, au cours de ce Xe Congrès international nous nous sommes instruits dans la Science que nous cultivons, nous avons fait aussi la connaissance d'une grande nation. Nous avons mesuré l'ampleur des efforts accomplis par nos hôtes dans les domaines de la science, de l'industrie et de l'agriculture. Vous êtes jeunes, Messieurs les Canadiens, vous êtes forts. La foi en vos destinées vous soulève et vous porte vers un avenir de prospérité.

Votre gouvernement a compris le rôle capital que la recherche scientifique, créatrice de progrès théoriques et pratiques, tient dans la vie des nations. Il la favorise largement et j'en suis sûr amplifiera encore les moyens qu'il met à votre disposition. Notre visite au Conseil national des Recherches nous en a donné la preuve. L'entomologie a pour la protection et l'exploitation de vos immenses richesses agricoles une importance primordiale, aussi avez-vous su la développer relativement plus que dans tout autre pays. Tout cela, Messieurs, est à votre honneur et je souhaite que votre governement, en ayant une juste idée de l'évolution du monde moderne, vous aide de plus en plus pécunièrement et moralement.

La Science prend une place grandissante dans la vie des sociétés humaines. Sans doute faut-il s'en réjouir, car elle accroît l'emprise de l'Homme sur la Nature, crée de nouvelles richesses et réduit notre peine.

Nous aimerions, Mesdames, Messieurs, que la Science fut plus généreuse encore et apportat à l'Homme ce dont il a le plus besoin, la Sagesse. Elle n'est en soi ni créatrice du bien, ni génitrice du mal. Elle ne prend sa valeur morale et sociale qu'en fonction de notre propre volonté. Quoi de plus utile que la hache qui abat la forêt, quoi de plus atroce qu'une hache lorsque Caïn en frappe son frère Abel.

L'Ordre dans la Nature nous apparaît souvent comme inexorable et fatal dans son déterminisme. Mais, l'Homme, s'il sait utiliser la Science, peut faire régner chaque jour plus de justice et plus de bien-être au sein de ses sociétés. Pour cela, il faut qu'à chaque instant, il soumette son savoir à des règles morales justes et saines. Sans cette indispensable précaution, la Science risquerait de plonger l'Humanité dans les ténèbres des destructions infernales, et sans aller aussi loin dans le pessimisme, exalterait l'égoïsme et la soif de jouir. La Science, si souveraine soit-elle, doit s'incliner devant les règles morales. Hors de cela, elle ne serait que l'instrument du mal.

Au biologiste qui détient le redoutable pouvoir de modifier l'être vivant et qui, bientôt peut-être, n'hésitera pas à changer l'Homme lui-même, s'adressent tout particulièrement les recommandations de prudence et de sagesse. Rien de ce que nous faisons n'est sans importance. Rien ne nous permet de prévoir ce qui résultera de nos découvertes même de celles qui nous paraissent être futiles.

L'entomologiste qui vit dans la joie de la découverte des inépuisables beautés de la Nature est incliné à l'optimisme et ne vise point à nuire à son prochain. N'est-ce point là un des charmes et une des vertus de la science que nous cultivons et aimons?

TECHNOLOGICAL RESEARCH

Il faut, Mesdames et Messieurs, que nos réunions internationales soient pour nous une occasion non seulement de devenir plus humains, mais aussi de mieux mesurer les responsabilités de l'Homme de Science.

Je suis convaincu que le Xe Congrès international n'a failli à aucune de ces tâches essentielles. Aussi, Mesdames et Messieurs, puis-je en toute tranquillité d'esprit lever mon verre en l'Honneur de l'Entomologie et de nos hôtes canadiens.

DR. GLEN:

Mr. President, honoured guests, ladies, and gentlemen:

This is, I believe, the largest number of entomologists ever assembled in one convention. I am indeed delighted and greatly honoured to address you. To do so, even for ten minutes, is a distinct privilege. Actually, it would take six weeks on standard office hours to speak with each of you in turn for the same length of time. Given these facts, our administration had no alternative to putting me on the program.

In our attempts to understand insects, we entomologists have tried everything from a study of fragmented specimens on slides and in tubes to investigations of whole populations in natural habitats. But in all instances the long-range objective is the same: to interpret natural phenomena and to communicate the information to others. My remarks this evening will be confined to reflections on a few relevant concepts as discerned from behind the desk.

Concepts, of course, are simply ideas or opinions. They are usually derived through wide experience and therefore are usually widely applicable. Concepts reflect points of view and attitudes, but they are not principles; and in reference to natural phenomena they should not be confused with the so-called natural laws, the discovery of which fires the ambition of every biologist. However, since there are relatively few established principles in the biological sciences, working concepts become a very useful, and indeed necessary, substitute. They provide the essential framework on which to orient our thoughts and thus to gain perspective in our various fields of interest. In my opinion, the importance of working concepts in research and in research direction cannot be overestimated.

But every worker must develop his own concepts. Much of their value lies in the struggle required to think things through to an acceptable conclusion. A concept usually evolves slowly and may never quite mature, especially if it concerns the dynamic subject of nature. However, conceptual thinking can be applied to other than the philosophical aspects of research, as for example to our general ideas of a project and of a scientific paper. Let us examine these briefly.

We are not concerned here with the academic question "What is a project?", but rather with the concept of a project in relation to a larger program of work. In my opinion, it is helpful to regard every research project as a unit, a unit of endeavour that begins with a hypothesis or an objective and ends with a report or a publication. Between the beginning and the end there is no proper stopping place. It is important in training the junior officer to recognize that writing is part of research and to present this viewpoint to him while he is developing his concept of a project.

Unfortunately, scientists rarely study the fundamentals of writing. But there is just as much need for a good working concept of a scientific paper as for other concepts in research. Study, practice, and frequent criticism by colleagues will bring surprising rewards. Everyone should aim at a standard in writing; and publication should be undertaken early in one's career. Frustration and lack of confidence frequently overtake the worker who habitually puts off the final act of writing up his results.

Now let us turn to more philosophical considerations. I believe that we live in an ordered but ever-changing world; and, as biologists, our ultimate objective is to understand the laws that govern these changes. In approaching this task, it is helpful to orient oneself within the universe and to establish to one's own satisfaction the necessary working concepts.

For example—and may I speak in very general terms and be forgiven for oversimplifying—, I look upon the universe as an indivisible complex of countless forms of matter and energy in which no species of plant or animal exists in total isolation and in which no factor, physical or biotic, operates in complete independence. My concept does not admit of any overriding subdivision of purpose behind the laws of nature, such as to produce gravity or magnetism or radioactivity or even to produce life. Instead, I prefer to give the natural laws the all-embracing purpose of supporting the total complex that we know exists and that we have come to call *nature*. Hence, within my concept of nature I would include man and all things pertaining to him. In fact I exclude nothing from my concept of nature for I regard the universe as a unity.

I also look upon this concept of the oneness of nature as a master concept with very wide application. For example, it is as suitable for reference to parts of the universe as to the whole universe. Thus the natural laws that govern the composition of any community (whether you call it a biome, an ecosystem, or a habitat) must embrace *all* the forces that impinge on the community both from within and from without. Likewise, the density of any population of insects at any given time must be a product of the interactions of all concurrently active factors, each of which, of course, differs in time and space and in effectiveness. Or, again, an adequate concept of a species must include all observable features throughout the life stages and all relationships throughout the distribution range. To implement this concept fully would mean the describing of our species in detailed physiological and ecological as well as morphological terms. This would be a colossal task in which for each species the methods of experimental biology would have to be applied to populations from different localities. But I am afraid we must face up to it. The economic entomologist usually is much more concerned with the local populations in his orchards or grain fields or woods than he is with the species as a whole. To serve him satisfactorily we must know the variation in behaviour, tolerances, etc., within the species and whether he is working with one or more distinct biotypes. To achieve this requires the combined efforts of physiologists, geneticists, ecologists, and systematists for, of course, we need the *whole* picture. Meanwhile, let us hope that we do not find our basic taxonomic entity to be as illusive as the physicist's basic particle, which I understand has now become virtually inseparable from the basic energy unit. But behold! What could lend more support to the concept of oneness of nature than the fact that substance and energy appear to be inseparable, whether we are dealing with the infinitely small or the infinitely large?

So far, I have applied this general concept to entomological problems. But if nature be truly one, the concept should be equally applicable to other components of the universe, to man and his problems, for example. I think that it is. Surely, the key problem of our day is effective recognition ot the oneness of the human race; and the key task before us, the building of one world for mankind. I shall not attempt to suggest how this might be achieved, but I would suggest that we have the necessary concept if we can only mature sufficiently to bring it to reality. Of one thing I am certain: we can never build one world by playing one part of humanity against another; or by emphasizing a philosophy or ideology that extols a portion instead of the whole, such as glorifying the individual or the race or the nation or the economic class. Such an approach fragments humanity and is at variance with my basic concept.

However, the point that I wish to emphasize is that we, both as scientists and as individuals, contribute best by having long-range goals towards which we direct our efforts. These not only give purpose to our work and to our life but also insulate us against adversity and frustration. Goals such as the complete understanding of our insect species and how to regulate their abundance or the building of one world for mankind are admittedly far beyond our grasp, perhaps even for generations to come. But if we believe that they are worthy goals and that our efforts are in the right direction we should be encouraged to continue and to continue with enthusiasm. We well might conclude that we are fortunate to be participating in such a noble crusade. We might even agree with Sir James Jeans that "To travel hopefully is better than to arrive".

Mr. Fowler:

Mr. Chairman, distinguished members of this conference, ladies and gentlemen:

I need only take a few moments to say what I have to say.

I am here tonight to represent the Executive Board and Members of the Canadian Pulp and Paper Association and to tell you now happy we are to be your hosts this evening. This is perhaps to be taken as an evidence of the interest of the pulp and paper industry of Canada in the work of entomologists. While our interest is naturally more specially in the field of forest entomology, we realize that all branches of the subject are important and interrelated and all deserve support.

It may interest you to know that this concern of the Pulp and Paper Association in entomology is not a recent thing. Just after the war, we took a leading part in bringing about the establishment of the Forest Insect Control Board—which was, I think, the first venture in co-operative work in forest entomology between the Dominion Government, the provincial governments and our own industry. We have joined with the Canadian Lumbermen's Association and the British Columbia Forest Industries in giving scholarships to students in forest entomology.

We do this, of course, because of our great interest in forest conservation and our concern over the losses from forest insect damage. In the past, this damage may not always have seemed serious because of Canada's great forest reserves. But in the future, these losses will vitally affect the very existence of pulp and paper mills as we move forward and plan for complete utilization of our forest resources.

Not long ago we made a submission to the Royal Commission now studying Canada's Economic Prospects over the next 25 years. In this brief, we estimated that the demands likely to be made on Canada for pulp and paper products will double in the next quarter century, and will require twice as much pulp wood as we are now consuming. We estimated that the supply of wood can be sufficient to meet this demand, provided Canadian governments and Canadian industries take the proper steps to protect, and conserve and manage our forests. One of these steps must be the reduction in forest losses from insect damage and we look to the members of this conference and other entomologists throughout the world for assistance in achieving this result.

From the appreciable amount of time you have given in your discussions to problems of forest entomology it is quite evident you are aware of the importance of these problems. It is an international problem and calls for this type of international discussion. However, I am glad to have this opportunity to urge you to continue your work and efforts in the future.

I wish you great success in your deliberations at this conference.

We are glad to have you as our guests at this Dinner and hope that you enjoy yourselves very much indeed.

The Guest Speakers were introduced and thanked by the President.

On Friday, August 24, after the close of the scientific sessions, the members of the Congress were entertained in the Great Hall of the Université de Montréal to a Vin d'Honneur, in the presence of the Rector, Monseigneur Lussier.

The morning of Saturday, August 25 was devoted to the final scientific sessions, the afternoon to the closing plenary session. At this session, Professor V. P. Wigglesworth, the leader of the delegation from the United Kingdom, gave the following short address containing the resolutions prepared by the Resolutions Committee.

PROF. WIGGLESWORTH:

The Resolutions Committee is a Committee nominated by the President and made up of representatives from some thirteen national delegations. We have held one meeting and I have been instructed to bring forward four resolutions.

1. The first is an expression of condolence with Mrs. Dunavan on the tragically sudden death of her husband, Prof. David Dunavan of Clemson College, South Carolina, while both were attending this Congress.

2. Secondly, we wish to recommend that in any future Congresses special attention should be given to the provision of a translation service. The detailed arrangements for such a service would, of course, depend on local circumstances.

3. Thirdly, we recommend that at future Congresses the scientific communications should not be printed in full, but only in the form of brief summaries of an agreed length. Such summaries would indicate where the full publication could be found. This resolution received the unanimous support of the Committee.

4. Our fourth resolution is a very important one. It is a resolution of thanks to all those organizations and all those individuals who have been responsible for arranging the Tenth International Congress of Entomology.

This Congress has been of unprecedented size; and this fact by itself makes it quite impossible for me to express adequately all the gratitude we owe to everyone concerned.

We wish, however, to express our thanks to McGill University, to the University of Montreal and to the Protestant School Board of Montreal for the provision of accommodation both for the Congress and for many individual delegates—and for many other courtesies

We wish to thank our hosts for the many social functions they have so generously provided: the City of Montreal for the Chalet supper; McGill University for the Garden Party; the Canadian Pulp and Paper Association for the Banquet; the University of Montreal for the "Vin d'honneur"; the city of Quebec for the entertainment they provided; and the Department of Agriculture and the National Research Council for our entertainment at Ottawa

You have before you in the Programme the printed lists of the Committees of the Congress. Amongst so much service, freely given, it is no easy matter to frame an expression of our thanks that will be inclusive without being invidious.

First and foremost we are, of course, indebted to yourself, Sir, as our President. I believe we can perceive your wise influence in the scientific programme. I know that you gave us a Presidential Address which has made us all think. And I know that your good humour has done an immense amount to keep the wheels running smoothly.

Of our vice-Presidents, Dr. R. Glen, President of the Entomological Society of Canada (who are our hosts) has provided valuable assistance to the Congress in all kinds of unrecorded ways; and Father Fournier has proved an invaluable intermediary between the Congress and the City of Montreal and the Province of Quebec.

Turning now to some of the special arrangements for the Congress, I must mention the organisation of the excursions, most of them still to come, which have been so skillfully planned by Mr. H. L. Seamans and his colleagues on the Excursions Committee.

I have been told also that I must express emphatic appreciation for the arrangement of the Ladies Programme, and for the care that has been provided for the children—a novel feature in our Congresses. In this connection I must mention particularly Mrs. J. Stanley and Mrs. J. W. Boyes and their Committee.

The Montreal Committee was responsible for the local organization of meetings and accommodation and all the detailed arrangements for the operation of the Congress. I am sure that all will agree that this has been a masterpiece of organization. Many have been concerned in it, but I must confine myself to mentioning the names of Dr. J. Stanley and Brother A. Robert.

The Programme Committee, under the chairmanship of Mr. G. P. Holland, have displayed remarkable skill in the grouping of the scientific contributions.

Besides its sheer size, this Congress has been characterized by another unprecedented feature: the extent to which funds have been provided to bring delegates from overseas. I believe that that has been money well spent: it has provided a unique intellectual stimulus to a wide cross-section of the entomologists of the world, and it has enabled them to see something of the remarkable advances being made by Canada in the field of entomology. As you will already know, Mr. A. B. Baird and Mr. W. N. Keenan were able to recruit a great band of collaborators who collected the necessary funds. The list of the contributors has been printed in the programme; to all we express our thanks.

Finally I come to what must always be the king-pin in the Congress—the Secretariat. I have been repeatedly told, and I know it to be true, that this has been a collective effort and that all members of the Secretariat have pulled their full weight. We are most grateful to them. But I also know that Mr. Antony Downes has been on this job from the outset, and that for a year or more he has given virtually his whole time to the arranging of this Congress. I think I can do no more than assure him that we really do appreciate all he has done for us and for Entomology.

Before I conclude this list I am sure you would wish me to make special mention of the Boy Scouts and all the other volunteer helpers too numerous to name.

In conclusion, I should like, for a moment, to go beyond my instructions from the Resolutions Committee and express a personal comment on the Tenth International Congress of Entomology.

Entomology has much to contribute to the material welfare of mankind; there is a struggle between man and insect for the domination of this planet. And I am sure that our deliberations have contributed towards the final victory of man. But we should not forget that these Congresses were initiated by men who were fond of insects. Many hundreds of our present delegates are here simply because, for some unaccountable reason, they take a passionate interest in this group of animals. Others find among the insects ideal material in which to study the most difficult and fundamental problems of biology.

It will be an unhappy day when these enthusiasts are forgotten and we think of entomology solely as a means to human comfort. And it will be a bad day for economic entomologists when they cease to draw inspiration from the teaching of taxonomists, physiologists and ecologists.

To me it has been encouraging sign, that in spite of the enormous predominance of economic entomology in North America, the fundamental sciences of entomology should have figured so prominently in our deliberations.

The resolutions proposed were accepted by acclamation.

Mr. N. D. Riley, Secretary of the Permanent Committee of the International Congresses, then presented to the Congress the results of the deliberations of the Committee. These were as follows:—

Mr. Riley:

There are a few matters which the Permanent Committee or the Congress needs to bring to the attention of Congress.

First, it has to report that in the interval since the ninth Congress was held in Amsterdam in 1951, it has attended two General Assemblies of the International Union of Biological Sciences acting in its capacity of Entomological Section of that Union. The first of these Assemblies was held at Nice in 1953, the second at Rome in 1955. The Proceedings of these meetings have been, or will be, published by the Union.

Secondly, it has to place on record its regret that it was not found possible by our Brazilian colleagues to make good their invitation, which had been accepted by the Permanent Committee after the last Congress, to meet in Brazil in 1955. This regret has been wonderfully tempered by the magnificent success of this Congress in Montreal, which is now drawing to a close.

It is customary on this occasion for the Permanent Committee to recommend Congress to elect to honorary membership one or two distinguished entomologists who have not only world-wide repute in the science, but also a lively and active interest in the welfare of the Congress. Accordingly, they recommend Professor J. Chester Bradley of the United States of America and Dr. A. da Costa Lima of Brazil be so elected.

A matter more closely concerning the Permanent Committee also needs the approval of Congress. The Committee has been so kind as to accept my resignation as Secretary of this Committee; in my place they recommend that Dr. D. J. Kuenen of Leyden, Netherlands, already well known to you as the very able and affable President of the ninth Congress, be elected Secretary. Dr. Kuenen has already signified his willingness to serve.

Finally we come to the 11th Congress. Several attractive proposals have been received. After careful consideration of all the issues involved, the Permanent Committee recommends that the Austrian invitation to meet in Vienna in 1960 be accepted.

The recommendations of the Permanent Committee were also accepted by acclamation.

Finally Dr. Karl Schedl, on behalf of the Government of Austria, confirmed to the Congress the invitation to hold its next meeting in Vienna. This was accepted by the Congress.

The President of the Congress then thanked the members for their help and cooperation and declared the Congress closed.

However, following the Congress a number of important excursions listed in the Official Programme were arranged and these were well attended.

PLENARY SESSION

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Editor
W. R. THOMPSON

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Reminiscences of an Entomologist

By Karl Jordan
The Zoological Museum
Tring, Herts, England

Mr. President, Members of the Tenth Entomological Congress:

When my friend Norman Riley informed me that the Tenth International Congress of Entomology would meet in Canada, the prospect of visiting your country attracted me very much, for I had had only a glimpse of it in 1928 when members of the Fourth Entomological Congress went to see the Niagara Falls. However, my endocrines, the guardian angels which look after the proper functioning of the processes of life, soon left me in no doubt that owing to the wear and tear of the many past years, the old body would not be able to produce the energy necessary for attending the Congress. Then you, dear President, and your Organizing Committee came to the rescue by inviting me to address this Opening Meeting by means of a tape recorder. I thank you from the deepest recesses of my soul for thus making me an active member of the Tenth Congress.

Although the travelling days are over for the body, the mind roams the world, revisiting places where I collected, or reflecting on biological problems, which have become so innumerable since the Linnaean divinely created constant species has gone to the limbo to join Manitou and the other gods of old. I find no time for boredom at all.

It was nearly 80 years ago that I began to collect plants systematically, incidentally fell in love with a longicorn beetle[1], which one of my brothers had found in the forest in some numbers on the inflorescence of a *Sambucus* and thenceforth became a devoted coleopterist.

Like every field-entomologist I acquired as a schoolboy and undergraduate a knowledge of detail in the life of many beetles, concerning their environment, food and variation, detail bearing on evolution, and later on mentioned in faunistic or systematic papers, which one cannot expect a geneticist or student of evolution to read. For instance, in the forest south of Hildesheim, at the side of a brook where sand had accumulated, I found on the sand under flat pebbles a flat *Bembidion*[2], some specimens pitchy black, the majority dull metallic green. Accidentally pushing with my foot some of the sand into the brook, I saw specimens of another species[3] float about, bright green, very glossy and its elytra strongly convex. That *Bembidion* lived a few cm. below the other in the sand saturated with water.

As regards variation, the most interesting case I found (in the early days) is that of *Cicindela germanica*[4], a common species on cultivated ground, not confined to sand as are so many species of that genus. It is a small dull green species of which glossy metallic blue specimens[5] and pitchy black ones[6] had been known for a long time to occur in many districts. I have come across such specimens only in one place in the valley where I was born, and I collected them for a number of years as material for exchange with foreign coleopterists. They occurred on some acres of ground which slope up to the wood. I never counted the normally coloured individuals, but my impression is that about one in ten was either black or glossy blue. If the Mendelian breeding experiments with beans had at that time already been rediscovered, I would have put this variation of *Cicindela germanica* before my mentor in zoology, Professor Ernst Ehlers of the University of Goettingen.

There are other points in the variation of insects overlooked or neglected. Although all biologists seem to agree now that individuals are never absolutely identical, few seem to be aware that in bisymmetrical beings the left and right sides are likewise different. The study of variation therefore begins with a comparison of left with right, and this will inevitably lead to the conclusion that the life-processes of growth, division and regulation are only more or less correct, variability (i.e. flexibility) being a primary attribute of life.

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[1] A common species of which I later on learnt the name to be *Strangalia armata* Herbst; an earlier specific name is *maculata* Poda.

[2] *Bembidion tibiale* Sturm, 1825, Deutschl. Ins. V.: 127.

[3] *Bembidion stomides* Dejean, 1831, Spec. Gén. Coléopt. V.: 146.

[4] *Cicindela germanica* Linnaeus, 1758, Syst. Nat. ed. 10: 407, Germania.

[5] *Cicindela coerulea* Herbst, 1806, Kaefer X.: 182, tab. 172, fig. 4, Nordamerika (*sic*!); preoccupied by *Cicindela coerulea* Paykul.

[6] *Cicindela obscura* Fabricius, 1798, Ent. Syst. Suppl.: 61, America borealis (*sic*!).

As this question will be dealt with in a paper I am writing on *Stenoponia*, a genus of fleas, I confine further remarks on this subject to an omission which would have been avoided if I had prepared a paper on the mechanism of copulation of certain Lepidoptera for reading at the meeting of the Symposium at the Ninth Congress. Being deaf, I did not attend the Symposium, which discussed the great variation in the tail-end segments of the male insect and their frequent asymmetry. When at the turn of the century I was working at the revision of the Sphingidae it was discovered that the phenomenon of asymmetry in the genitalia obtained to a varying degree in both sexes in many genera of the (essentially) American subfamily Sesiinae and was most pronounced in some species of *Haemorrhagia*[7], (Nearctic and Palaearctic) and *Cephanodes*[8] (Oriental and Aethiopian). In the males of these Hawkmoths the left clasper is more or less reduced and the anal segment often much modified, and in the females the orifice of the vagina, which is normally central, is shifted to the left. As this change of position of the orifice is not indicated in species in which the male organs are but moderately asymmetrical, this evolution probably started in the male. And since the vagina of the Lepidoptera is part of the eighth abdominal segment, whereas the clasping organs of the male belong to the ninth and tenth segments, it is reasonable to conclude that the adjustment of the sexes to each other has been achieved by Natural Selection based on the plus-minus status of the morphological detail. The asymmetry discussed is by no means confined in Lepidoptera to some Sphingidae. I have found it in all the African and Oriental Syntomidae dissected and in some Arctiidae[9], and it would be worthwhile to study the tail-ends of both sexes of the New World Syntomidae, which I have not touched.

Before concluding this address I beg leave to remark that all general statements based on one or a few species are suspect and require affirmation by the study of other species. The number of insects being much larger than that of all other animals together, entomologists will never be short of work; but in hoping that this general statement will remain correct, we must also remain clearly aware that there have been and still are civilizations hostile to the study of nature and that even Aristotle had to flee from Athens in order to avoid the fate of Socrates.

The members of the Tenth International Congress of Entomology have my sincerest good wishes for a successful meeting and an enjoyable time in Canada.

[7] *Haemorrhagia* Grote & Robison, 1865, as applied by Rothschild & Jordan, 1903, in A Revision of the Lepidopterous Family Sphingidae: 438–460, tab. 51, fig. 17–21, tab. 52, fig. 4 and 5, in Novit. Zool. IX Suppl.

[8] *Cephonodes* Huebner, 1819, as applied by Rothschild & Jordan, l.c.: 460–471, tab. 43, fig. 22–25, tab. 52, fig. 1–3.

[9] *Utetheisa* Huebner, 1819; Jordan, 1939, On the Constancy and Variability of the Differences between the Old World Species of *Utetheisa*, in Novit. Zool. XLI; 251–291, text-fig. 226-255.

The Interpretation of Taxonomy

By W. R. Thompson
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Ottawa, Ont.

I trust I shall not wound the feelings of our English colleagues and disturb the harmony of this wonderful International gathering, if I say that the English have very generally regarded themselves as a nation of amateurs. They like to be complimented on the things for which they are not famous and which they do in their spare time. When I was in the University of Cambridge, many years ago, I spoke admiringly to the Professor of Zoology about the work of one of the entomologists in his department; but his reply was:—. "Yes, but have you seen his wonderful collection of pipes?"

I have not the good fortune to be an Englishman nor am I famous for anything in particular; nevertheless I think there is something to be said for the English attitude in that the view taken by the amateur though it may be uninformed, is sometimes interestingly unconventional. This is one reason why I have decided to talk today about the interpretation of taxonomy on which, of course, I have no claim to speak with the authority of many colleagues and friends here. Furthermore, the ideas I shall put forward are not basically my own,—I mean, are not original with me,—but are those of another amateur, so that you may consider that it is a case of the blind leading the blind.

However, I have an excuse for my discussion, which is that I am harking back to some remarks made by that versatile and acute entomologist Dr. Walther Horn, at the last entomological congress held in America: the Ithaca Congress of 1928. Dr. Horn, with whose name you are certainly all familiar, was associated with the International Congresses from their foundation until his death in 1939. His contributions to the meetings, says a biographer, were among the high spots of such sessions. He published over 280 papers on the Cicindelidae and there is no question about his status as a systematist.

In his paper to the Ithaca Congress, Dr. Horn expressed some views which form the starting point of my own talk. He said, in the first place, that the controversy between the Darwin-Haeckel tree of life and the opposite hypothesis of fully isolated and only parallel lines of evolution of all species, will be cleared away, if ever, in the far future by new hypotheses. He added, that the greatest taxonomist whom the world had seen up to that time was Charles Linnaeus: he created his system not from the phylogenetic standpoint but from the analytic standpoint of relationships. That, said Dr. Horn, is why he created the picture of the "torn net". Dr. Horn considered, that if you interpret Linnaeus' comparison of a "torn net" as a symbol of phylogeny, it would prove that the organic world is radically polyphyletic.

It is of course clear from statements made by other entomologists at the Congress, that the objective of taxonomy was generally regarded as the reconstitution of family trees and I think this is still the prevailing conception. The taxonomic picture is interpreted in terms of evolutionary theory, usually of the Darwinian type, and the possibility of this interpretation is advanced as a proof of the theory. A common expresssion of this view-point is the statement that the taxonomic system becomes *intelligible* only in terms or evolutionary theory. The morphological gradations in organ-systems, the so-called rudiments, the intermediate forms with unusual features, lend themselves particularly well, it is considered, to this interpretation. However, when Dr. Walther Horn delivered his paper, he was certainly perfectly familiar with all these considerations and meant his remarks to be taken seriously, whether they were accepted or not. More recently, Blackwelder and Boyden (1952) have expressed sympathy with the Linnaean view of taxonomy, in so far as they say that it should group the objects of study in accordance with their essential natures.

We have therefore, I venture to think, sufficient reason to consider any interpretations of taxonomy based on the Linnaean or polyphyletic concept—the concept of the taxonomic system as the "torn-net".

Such an interpretation is to be found in the little-known but very original work of Giovanni Schiaparelli, entitled "Studio comparativo tra le Forme Organiche Naturali et le Forme Geometriche Pure", published in Milan in 1898.

Giovanni Schiaparelli was a distinguished Italian astronomer well known for his observations on cometary orbits, double stars, the so-called canals of Mars, which he was the first to describe, and his studies of the astronomy of the Hebrews and Babylonians. He was an able mathematician who became interested in the problems of organic form through his conversations with Professor Tito Vignoli, then Director of the Natural History Museum in Milan. The essay I have mentioned seems to have been his one and only contribution to biological theory. Having said his say, he returned to his astronomy.

It is difficult, in a short talk, to do justice to Schiaparelli's lucid and logical exposition nor is there time to examine it in detail. Perhaps it will be best to indicate his fundamental thesis, the reasons in favour of it and the consequences which flow from it, reducing the mathematical developments to a minimum because these can be studied in his original work and we can be sure, at all events, that the mathematical reasoning of Schiaparelli is impeccable.

The starting point of Schiaparelli is a datum of observation; to wit, that although for evolutionary theory the organic world is a continuum which for purely accidental reasons shows gaps of various dimensions, yet as it is, here and now, it is a discontinuous system. In this it resembles the inorganic world in which, on the whole, modern chemical investigations have revealed an orderly discontinuity whose existence the ancients did not suspect. In various ways the system as described in the text books of my youth has been considerably modified and complicated but we can still recognize definable groups of clear-cut entities which are, as it were, the building-blocks of the organic world. The organic world itself, as I have said, is composed of these separate and definable entities so it is reasonable to describe it as a world of fixed types—taking it, at least, as it appears to us *hic et nunc*. That the individuals of each type present variations does not fundamentally alter this fact, particularly since the biometricians have succeeded in bringing the variations themselves into the compass of laws.

To describe a morphological characteristic by a frequency curve is not really to describe it as indefinite; it is, rather, to establish a morphological law based on knowledge that is both detailed and accurate and, thus, to perfect the definition. To decompose a population into genotypes is an operation of the same character; since it consists in pushing the level of the definable into an area formerly regarded as containing no definite elements. Taxonomy therefore, even as perfected by modern genetics, still presents us with an orderly arrangement of definable and distinct types and the fact that the individuals of these types are built up as combinations of the chemical elements, which unite according to definite laws, enables us to understand why definable types exist and why they can be classified.

It is hardly necessary to say that I am not attempting to maintain, against the mass of evidence to the contrary, that everything the systematist calls a *species*, is a fixed and unalterable entity; or, indeed, to identify the "type" referred to, with any particular level of the taxonomic system. On the other hand, it seems true to say that the systematists, in general, do try to define and usually succeed in defining what they call "species" and the geneticists, in general, do not differ radically from them in regard to this particular point. "Species", says Dobzhansky (1951), "are tangible natural phenomena". This statement is philosophically inaccurate and considered out of context gives a misleading impression of Dobzhansky's views. Like the palaeontologist Gaylord Simpson and many other orthodox evolutionists, he recognizes the marked discontinuity between living forms both actual and extinct, yet he believes that they have all arisen by a gradual process, involving minute mutations. Microevolution, such as can be observed experimentally, is, he considers, the only possible explanation of macroevolution.

Like most geneticists, he holds that the hereditary determinants or genes are extremely numerous and the number of homozygous gene combinations is astronomical. This fits the idea of evolutionary continuity. Dobzhansky says, however, that "only an infinitesimal fraction of the possible gene combinations can be realized" and that "probably the vast majority of the potentially possible ones are discordant and unfit for survival". Furthermore although the geneticists make bold generalizations about the origin of morphological types, their claims to have observed the appearance even of "new species" acceptable as such to the systematist, are extremely modest and that in spite of the fact that the specific definitions given by the systematist are not always as clear-cut as he could wish. This is of course why zoologists like Caullery (1948) have decided that the solution of the problem of evolution cannot be found in the domain of mutations; and that the results of modern genetics merely relate to intra-specific phenomena. The production of new types, says Grassé (1938), must have occurred at very infrequent periods, by a kind of explosion, involving, therefore, profound but very rapid morphological changes.

It does, therefore appear, after due consideration has been given to the results of modern genetics, that we must accept the objective and very general fact of taxonomic discontinuity in the present as in the past and this is all that is required in the present discussion.

Perhaps it will be said that as more material,—living and extinct—is collected, the discontinuity tends to disappear which supports the idea of genetic continuity. But this is clearly incorrect, because research similarly filled in the table of Mendeleef, though the chemical types are quite distinct. Furthermore, when we consider such forms as the dinosaurs, we are inclined to feel that their discovery introduced distinct new types and, indeed, distinct new groups, extending and diversifying the existing categories but not unifying them internally. It is evident also that if we have two species, A and B, belonging to a given genus, and a new species, C, is discovered, it will have the same generic characteristics but will differ from the other species by excess or defect in certain characters. With respect to the two species and a given character it will either be in excess or defect as compared to both A and B in which case we may have graded series A B C or C A B or it will be in excess as compared with one and in defect as compared with the other which will give the graded series A C B. So it is, that as the range of collection is extended into different environments and new species appear, series in which gradations appear are to be expected; but this work on the whole, has not effaced the distinction of species but on the contrary has increased the list of species; has not replaced the system of types by a continuity but has multiplied these types.

For the sake of the argument and without prejudice, I shall therefore assume this discontinuity, discard the current view that the characteristics of organisms must be explained on a genealogical basis and consider, with Schiaparelli, whether a system of fixed types originating as such, can exhibit the peculiarities now generally explained on an evolutionary basis.

The chemist feels that he has acquired a basic knowledge of the substance he is studying, when he has discovered its *formula*! His idea, I think, is to establish a connection between the formula and the properties. The ultimate objective is to interpret the structural formula in terms of physical laws and express it as a mathematical formula. If it is legitimate to regard the properties of an organism also as the expression of a physical law, corresponding to the typical morphology, then a comparative morphology and finally, a taxonomy, based on mathematical law, is at least conceivable and from this point it is not a great step to consider the laws which reign in assemblages of pure mathematical forms,—more precisely, pure geometrical forms—and to enquire, as I have said, whether these laws, if they reign also in the world or organic forms, will not explain many features of the taxonomic system and many morphological peculiarities, which have been usually considered as explicable only on the evolutionary hypothesis and regarded, therefore, as arguments supporting it.

Since he regarded the taxonomic system as based on the existence of classifiable types, Schiaparelli considered each type to be the expression of a specific law. He considered it, therefore, as comparable to what is called, a *pure geometric form*. A pure geometric form is one characterized not merely by the fact that, as the philosophers say, it abstracts from matter, but by the fact that all its points are derived from one single law. The circle for example is a pure geometric form, as is the surface of the sphere or the ellipsoid of revolution; but the cube and the triangle are not. A cube may of course be the expression of some physical law as in the case of certain crystals; but its mathematical origin is complex and therefore mixed forms do not lend themselves well to the investigation we desire to make.

Examples of pure geometrical forms can be found either among lines or surfaces. The lines may extend into the three dimensions of space—an example being the helicoid. The surfaces offer great morphological variety and as D'Arcy Thompson showed many of these are duplicated in organismal forms such as the Protozoa.

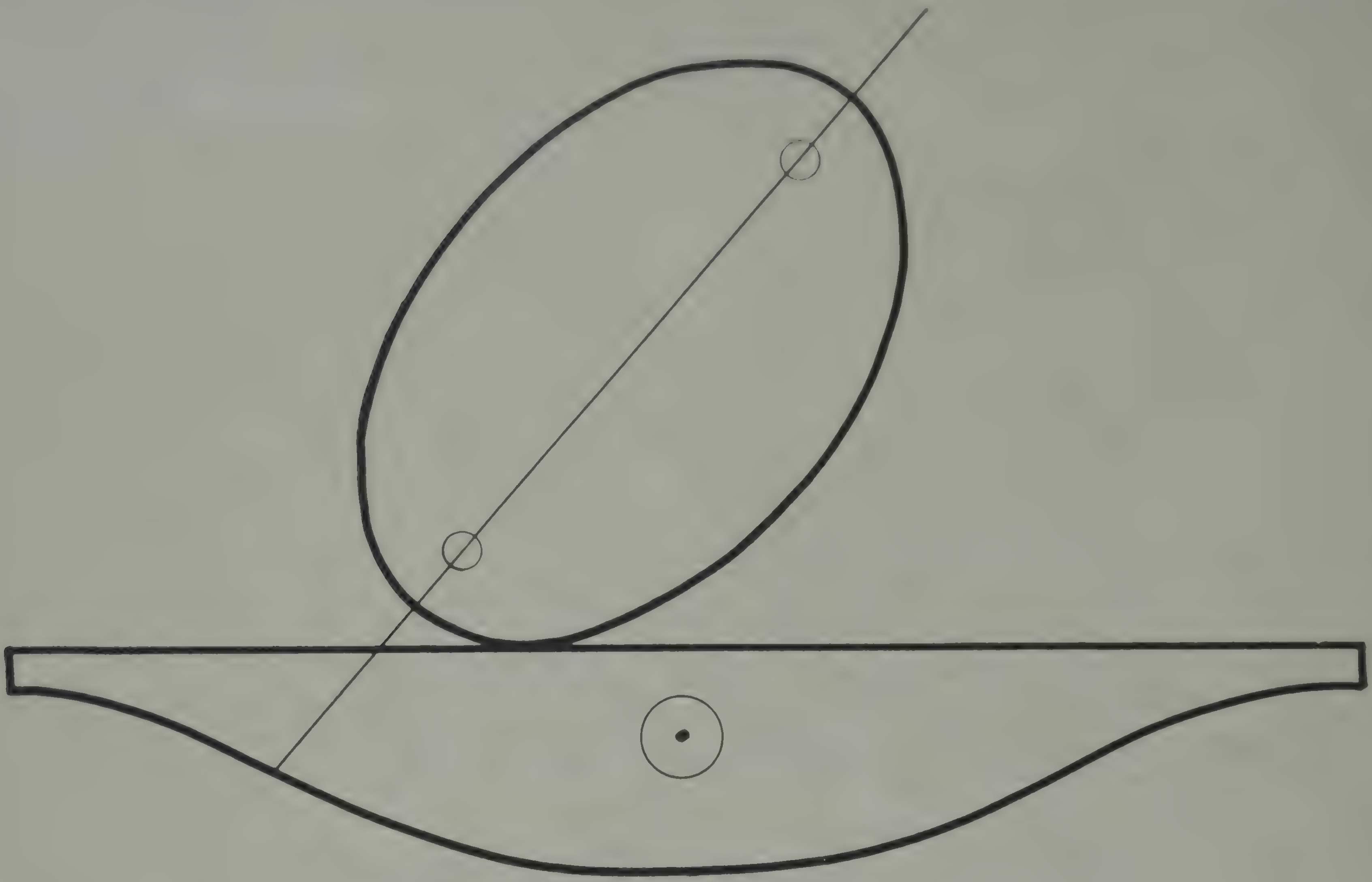

CHART 1

It should of course be said, once for all, that the mathematical generation of the form is profoundly different from its physical generation. Chart 1 may serve to illustrate this point. As the ellipse rolls along the base line, one of its foci traces out the curve I have drawn below the line, which is the unduloid. Inserting a nucleus as I have done, we get what is the outline of a hypodermal cell in a dipterous larva like Calliphora; but here the form is produced by the force of surface tension. On the other hand we can envisage, though I cannot produce, a mathematical development which would represent these forces in action so that physics and mathematics would coincide. To develop the basic principles he wished to explain, Schiaparelli took only the simplest cases, even as representatives of

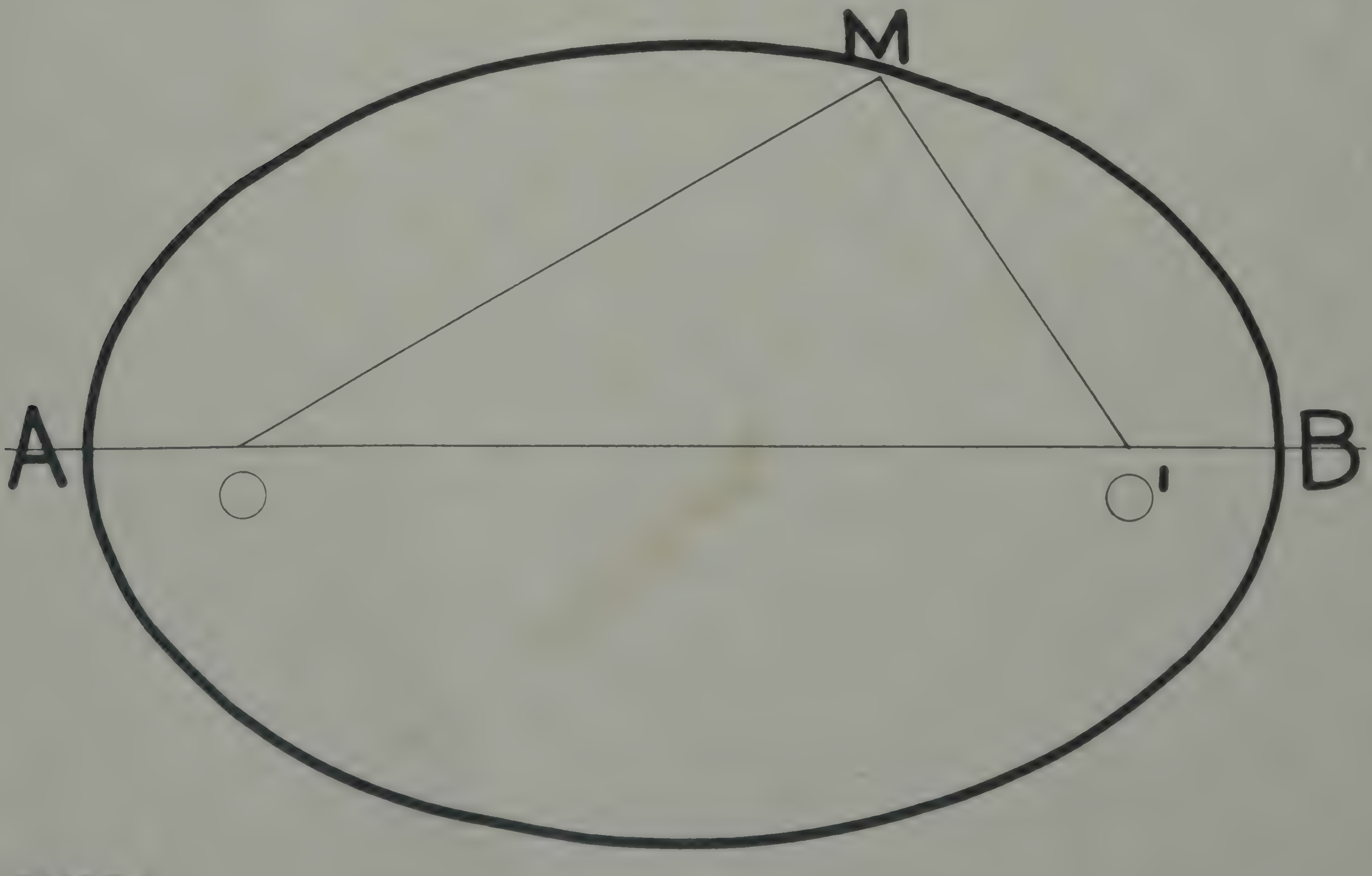

CHART 2

the plane curves. Taking, first, examples like the circle and the ellipse he showed that while each has a certain fundamental or typical character, corresponding to a certain algebraical *formula*, its peculiar, specific manifestation of this form depends on the value of certain algebraical constants known as *parameters* which we might also call determining factors. For example, taking the Chart 2, the distance 0 0′, may be called the parameter *a;* the sum of the distances O M, O′ M, the parameter *b*. Given these values, the ellipes is completely determined. Because of the values these have, one ellipse may be very long and narrow, while another is almost a circle; and yet both are ellipses. The visual differences between the various species of the genus ellipse, though they correspond to distinct mathematical representations are very slight and for the biological morphologist unsatisfying. For a presentation satisfactory to him one ought to choose and represent forms more strikingly varied. This could be done. The algebraical curves of the 2nd, 3rd, 4th and 5th . . . . orders can in certain cases be cut by a straight line in 2, 3, 4, 5 . . . . points so that a great variety of forms is clearly available here and with them it would be possible to give a visual exemplification of Schiaparelli's findings. Unfortunately, the task of constructing suitable curves is laborious so we must continue to rely on the general but abstract arguments he developed. To simplify the discussion let us consider a discontinuous system of curves having only two parameters and let us suppose that one of the two parameters (a) has a fixed value which is however only one of a series of values that it can have. Varying the other parameter (b) and giving it successively all the values it can take the points represented by the forms thus obtained will be arranged in a row and will form a regular series V1, V2, V3 . . . . traversing the system from one side to the other. The types of curves represented by these points having a common parameter will show a certain morphological relation which would not exist between two types taken at random in the system and differing from each other by both parameters. Furthermore it is obvious that in the same series V, V1, V2, etc. the morphological changes will occur regularly and gradually from one type to another.

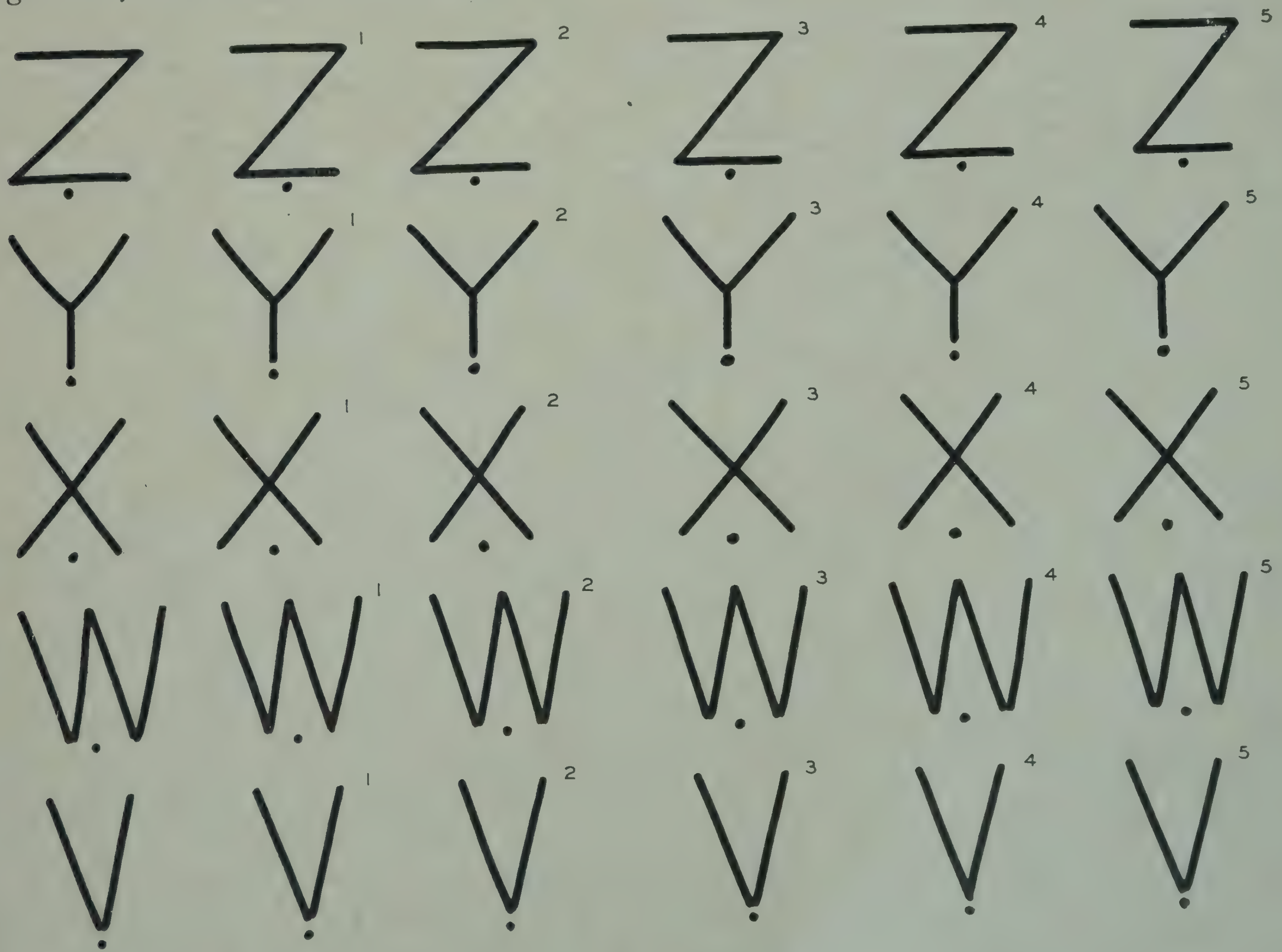

CHART 3

Now it is obvious we can make as many series of this kind as the parameter (a) can have values. We will thus have in addition to the series V, V1, V2, V3, V4, other series W, W1, W2, W3, X, X1, X2, X3 etc. which will also be arranged regularly along lines parallel to those of the first series. The ensemble of the series obtained by giving (a) all its possible values, will constitute the totality of the system; every point in it will belong to a particular series. The types of every particular series will have among themselves, an especially close degree of relationship, depending on the parameter they have in common (Chart 3).

These reflections lead us to an important observation and that is that since we have two classes of series, one transverse, corresponding to one parameter and the other longitudinal, corresponding to the other, *every type of the system* will belong simultaneously to two series. Since in every series there is a special relationship or analogy of form, so every type in the system will be connected in four different directions with other types around it and will present in these directions two different types of relationship and this is why the series in question are called analogical series. It is of course evident that what has been said about systems with two parameters can easily be extended to more complex systems. If there were three classes of analogical series in each of which every member would have in common two parameters and would differ only by the value ot the third. Of these three classes of series, we could figure the reciprocal relations by saying that one runs sideways, one lengthwise, and one in depth. Every type of the system would belong to three analogical series and would be connected with neighbouring types in six different directions corresponding to three different types of analogy. If the parameters are N in number we shall have N classes of analogical series and each of which all the members will have in common the value of (N–1) parameters, that is to say they will differ among themselves only by the value of a single parameter and every type of the system will belong to N series simultaneously and will be connected with neighbouring types in 2 N directions corresponding to N different types of analogy.

The work of Schiaparelli, of course, contains both inductive and deductive elements. He could, on mathematical grounds alone, have regarded the whole organic world as based on a single formula or law and have postulated, on the ground that quantity is indefinitely divisible, a morphological quasi-continuity between the various points in the system, even though this has been accidentally disrupted. If he did not do this, it was because the facts, to him, suggested basic discontinuities and the existence of types between which transitions cannot exist—as they cannot exist between an ellipse and a spiral. You will find the same idea expressed in the work of D'Arcy Thompson and it is stressed in both editions of "Growth and Form".

That the taxonomic system is composed of types which are the expression of fundamental and invariable laws is an idea which certainly corresponds to objective appearances. The Darwinists, said the Czech biologist Emanuel Radl (1930), hold in theory that the word species does not correspond to an existing reality but in practice they go on discovering new species, as was done in pre-Darwinian days. The number of *basic* morphological types is relatively small and they have persisted not only over vast periods of time but in vastly different environments. Schiaparelli believed that the facts of regeneration, where a small and relatively simple part of an organ reproduces the complex whole, supports his view of that specific types are manifestations of specific unitary laws and embryological experiments such as were made by Hans Driesch showing that parts of embryos can reproduce the whole organism would be for him, indications in the same direction.

The representation worked out by Schiaparelli is that of ordered collections of entities conforming to the same morphological type-such as are in geometry, the ellipse, the spiral, the unduloid of revolution—because they conform to the same fundamental mathematical law, which in its turn expresses a physical law. But they exist as subtypes, each conforming to the law of the group in its particular manner. In the same way, the compounds we call paraffins, all conforming to a certain fundamental formula, exist each as a special sub-type so that the various members of the group constitute a recognizable family and yet differ, in certain definite respects, for example, in their melting points. Nevertheless, even the differential characteristics show a certain similarity because although a particular parameter may have different values, its character may remain qualitatively the same. Each entity in the system therefore exhibits an internal coordination of which the source is the formula; and has a certain complex relationship to the other entities, such that the group of them can hardly be better described than by the comparison to a net, or better, a framework, remembering that to approach the complexity of nature, we might have to regard this as "multi-dimensional". This multi-dimensional net-work of curves might properly be called a family.

We are dealing with taxonomy in a very broad sense, and also in a highly abstract manner. Nevertheless if we consider objectively the groups of living organisms with which we are most familiar, as they are here and now, we can agree, I think, that Schiaparelli's representation applies to them. The idea that in the organic world there are certain basic formulae corresponds to the existence of the morphological types we recognize. The idea that there are sub-types, depending on independent parameters, corresponds to the existence of the determinants called genes. We need not adhere to the belief that the gene is an objective and tangible reality; but we can certainly say that it is so regarded by most geneticists. We need not maintain that it produces its effect quite independently of the other genes. Geneticists consider that there is interaction between genes, that the effect may be a combination effect and that one gene may produce several effects. Nevertheless they hold that the genes are distinct entities which normally reproduce themselves unchanged. There is therefore sufficient support in modern genetics for the concept of parameters of organic form as defined by Schiaparelli. Proceeding therefore on the assumption that the representation is correct, we may then enquire what conclusions may be drawn from it and ask, also, whether these are verified in nature.

The first point that is verified in experience, as I have already said, is that the simple multilineal arrangements which are usually the basis of phylogenetic trees are quite inadequate with respect to the tremendous complexity of taxonomic relationships. This complexity is particularly evident in the group with which I am most familiar; the Diptera of the family Tachinidae. In many sections of this group the arrays of genera and species made on adult characters differ radically from the arrays made on larval characters. There is argument as to which arrangement is *natural*. The evolutionary-minded decide, say, that the arrangement on adult characters is, and then "explain" the larval arrays as a result of evolutionary convergence. The truth may be rather, that only when the arrays are combined, have we obtained a natural arrangement, which is natural, not because it corresponds to relationships of descent, which we cannot ascertain, but because it actually exhibits the multiple and radiating morphological connections as they exist here and now. When Dr. Snodgrass (1951) tells us after a life-time of morphological investigation of the most searching character, that the head characters of the arthropods will be seen to be so variously distributed and combined in the several arthropod groups, that they cannot be made to fit consistently into any theoretical scheme of Arthropod relationships he is, I think, telling us that taxonomy corresponds to the representation of Schiaparelli.

In the initial stages of taxonomy when there was little material available for study, the definitions of genera and species mentioned few characters and then the simple linear relationships used in phylogenetic trees seemed justified by the facts observed. As the material accumulated, differentiation required a more careful morphological investigation and the relationships between taxonomic categories became more and more complex with "connexions multiples et rayonnantes" as Cuvier put it. In other words as taxonomy developed, it took on the characteristics of the networks of Linnaeus and Schiaparelli.

Many good examples of this development can be found among the Tachinidae. The genus *Exorista* of authors in the works of the older Dipterists, such as Schiner, Coquillet and Williston was defined, on adult characters, as a reasonably distinct category. Schiner describes *Exorista* as composed of medium sized, black species, tinged with yellowish or whitish grey, of broad, relatively short build, sometimes with the abdominal segments reddish on the margins. The antennae are inserted above the middle of the eyes; the third segment is from two to six times as long as the second segment which is very seldom elongate. The parafacials are bare beneath the lowest frontal bristles. The facial ridges are ciliate at most up to the middle. The vibrissae are on a level with the margin of the mouth which is not prominent. The eyes are hairy.

A study of a number of species of this genus showed that on the basis of reproductive habit, eggs and larval forms, it could be divided into four different sections one constituting a distinct and isolated group of species while the others had all close allies in other genera. This indicated the necessity of taxonomic subdivisions. C. H. T. Townsend, says W. F. Sellers (1943), recognized 17 different genera in this complex. However, Aldrich and Webber in 1924, lumped many of these genera of the Exorista group, for which they adopted the name *Zenillia*. The reasons these two experienced dipterists gave for their action, have an important bearing on the present discussion. "Generic characters", they said, "should be those of more ancient origin, externally recognizable, and should exist in both sexes, although they be supplemented by others which do not meet these requirements. Whether a species lays small eggs we cannot consider of generic importance, as the complex reproductive modifications which are so striking in the great Tachinid group seem to us of very recent development here, and not correlated with any distinct characters in other parts".

To this, Townsend (1936) replied that "Zenillia of Aldrich and Webber is an impossible complex of 6 tribally distinct elements and constitutes the worst mixed genus of modern times". He maintained that "the micro-egg stocks certainly date back to remote geologic epochs" but added that "age does not enter into the question, which is purely one of fundamental differences"; and was convinced that differences in reproductive habit are of the greatest importance in taxonomy.

Since there is no satisfactory palaeontological evidence about the origin of the reproductive types in the Tachinids, the view that these are very recent developments as compared with the external adult characters (or the view that they are of ancient origin), has no factual foundation but is merely an inference based on the general uniformity of adult structure and the difficulty of delimiting groups on adult characters. The anatomical and physiological correlations in the reproductive system, egg types and habits, contrast very strongly with the functionally uncorrelated assemblages of chaetotaxic characters generally used in defining the Tachinid groups in the adult stage. Aldrich and Webber attempted to minimize the importance of reproductive types by remarks implying that the differences are on the level of those between chickens laying large eggs and chickens laying small eggs; but the suggestion is inaccurate and misleading.

Some progress has been made in defining groups with the same reproductive habits, on adult characters. The Echinomyiines, which deposit larvae on leaves and constitute, with respect to reproductive habit and larval anatomy a fairly clear-cut group, can, as L. P. Mesnil (1939) has shown, almost always be recognized in the adult stage and separated from the other true Tachinids by the bare prosternum, the absence of inner reclinate orbital bristles and certain other characters. The Dexiids also are usually recognizable on both adult characters and reproductive habits, showing a fairly definite affinity with the Echinomyiines. But even here exceptions have to be made. Several of the other groups formed by Mesnil, though they are easily recognizable on adult characters, are quite markedly heterogeneous with respect to reproductive habit and larval anatomy and, what is more, contain species much more closely resembling those of other groups than some of those to which they are supposed to be most closely allied. It cannot always be said that the larval and reproductive characters represent correlations which are definitely specific or generic.[1] Nevertheless the larval characters seem to have greater morphological *consistence*, so to speak, than the assemblages of adult characters defining the categories. This, however, is the view to which my specialized study of larval forms inclines me. The students of adult characters continue to regard the assemblages based on these as the really *natural* assemblages. Because of the uniformity in adult structure, some of these assemblages, though sometimes defined on characters that appear insignificant, do not appear as markedly heterogeneous. For example, the tribe called by Mesnil, the Phorocerini is separated from the tribe Salmaciini by the fact that the prealar bristle (on the side of the mesothorax) is distinctly shorter and finer than the other dorsal bristles on the thorax. This character is very useful in practice but even the subtribe Blondeliini is heterogeneous in regard to reproductive habits and larval forms. For example, *Meigenia* deposits flat undeveloped eggs; *Compsilura* and *Blondelia* have ovipositors with which they inject larvae into the host; *Erynnia* deposits larvae externally. The subdivisions in some groups of Mesnil's Salmaciini, are even less homogeneous as I have shown in discussing the affinities of *Eusisyropa blanda* O.S. The Carceliini, apparently well characterized by the form of the head, also contains species with quite different reproductive habits, eggs and larval forms and even the genus *Carcelia*, regarded by Villeneuve as a strikingly natural group, now appears to be heterogeneous with respect to reproductive habit; this, at least is the view of Mesnil. Among the

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[1] For example, the Tachinids depositing minute eggs on leaves exhibit a very definite and complex morphological correlation related to the reproductive habit; but this occurs in a large number of different species distributed among many genera. The adults, eggs and larvae are usually structurally different; but their specific and generic characters have, so far as one can see, no adaptive significance.

Carceliines as defined by Mesnil are species depositing thin-shelled eggs with larvae ready to hatch (e.g. *Calocarcelia orellana*, *Carcelia processioneae* Ratz.), species depositing microtype eggs on leaves (e.g. *Eusisyropa blanda* O.S.) and species depositing pedicelled, elongate eggs containing an undeveloped larva (e.g. *Carcelia amplexa* Coq.). The heterogeneity of the categories as defined by the older dipterists therefore still exists in spite of the great efforts made to eliminate it.

It has been suggested that if *Carcelia processioneae* has now a thin-shelled unpedicelled egg, this is because it acquired the habit of attacking caterpillars which live in a web and that in consequence of this it ceased to lay on the host. It appears that the larvae are deposited on the webs and then go in search of the procession caterpillars. It is true that *Carcelia laxifrons* which has a pedicelled egg, attacks the caterpillars of *Euproctis chrysorrhoea* which also inhabit a web; but it is explained that these feed during the day when they are accessible to the parasite, while the procession caterpillars are nocturnal feeders. Why the larva of *Carcelia processioneae* could not go in search of the host caterpillar after emerging trom a pedicelled egg, is not at all clear to me; but however this may be, the hypothesis really appears to have no foundation in fact and to have been produced simply in order to provide an appearance of homogeneity in a heterogeneous group, by the gratuitous supposition that if *processioneae* has not now a pedicelled egg, yet its ancestor had one. Although *processioneae* was for long separated trom *Carcelia* under the name of *Chaetomyia crassiseta* Rond. Mesnil felt obliged to define the genus so as to include it. Moreover it appears that another species which on adult characters agrees with the typical *Carcelias*, has unpedicelled eggs.

The larval forms of the Tachinids are still very incompletely known. However, even in the rather scanty material available, there are a good many morphological surprises. *Digonochaeta setipennis* the parasite of the Earwig, is placed by Mesnil with the Echinomyiines and in the possession of an armoured primary larva it agrees with the group. Nevertheless, the larva is of a remarkable and unique type very different morphologically from those of *Lydina* and *Dichaetoneura* placed by Mesnil in the same section of the Echinomyiines. Furthermore *Lydina* and *Dichaetoneura* are also markedly different. The strange earwig parasite *Rhacodineura antiqua* Meig., placed by Mesnil with *Brachychaeta* in the Brachychaetina, a section of his Masicerini, has, like the type genus, microtype eggs; but so far as is known is unique in its larval morphology, with tissues made up of very few but very large cells.

Generally speaking, the grouping of the Tachinid genera, as indicated by the synoptic tables, differs greatly from author to author. A few examples will make this clear. In Schiner (1862) the Tachinids (in a more or less strict sense) are first subdivided on a venational character—whether the first posterior cell ends in or near the wing-tip or at a distance from it. In Coquillet (1897) the first division is made as between forms with well developed palpi rudimentary or absent. In Pandellé (1897) the major division is between forms with hairy eyes and forms with bare eyes. Adams (in Williston, (1908)) adopted the primary division of Coquillett. Curran (1934) first subdivides on the vestiture of the squama, then on that of the propleuron then on the presence or obsence of infrasquamal setulae, then on the vestiture of the eyes. Mesnil's latest great subdivisions (1944) concern first the vestiture of the prosternum, then the character of the anterior supra-alar bristle.

It is true that the subdivisions of keys may be regarded as of merely pragmatic importance, having no deep-seated significance. Very frequently, however, the authors express or suggest the view that the groupings are *natural*, as compared, presumably, with other arrangements that would be *unnatural*. The terms natural and unnatural are indeed part of the normal vocabulary of systematists. Nevertheless, it is not easy to decide what they mean by these words. If pressed, they commonly reply that a natural arrangement is phylogenetic; that is, it assembles entities that are genealogically connected, so that the species of a genus might be regarded as cousins and the genera as more distant relations; the elements of the whole group forming, as it were, the branches and twigs of the family tree.

The fundamental and fatal objection to this interpretation, is that the systematic arrangement is not deduced from the family tree, but the family tree from the systematic arrangement; which is based on the morphology of the species existing here and now. To deduce systematics from phylogeny, the phylogeny must first be known.[2] In fact, even the ancestry of the family is not known, to say nothing of that of the subfamilies, tribes genera and species. The families of the Diptera are placed in a certain order based on morphological considerations which cannot really be substantiated by palaeontological evidence but derives its force rather from the arrangement of the orders of the insects, this again being based on the arrangement adopted for the Class insecta, the phylum Arthropoda and the invertebrate phyla morphologically most similar—for example, the polychaete worms. The factual basis of the arrangement is therefore not phylogenetic but morphological and depends on the fact that the forms can be arranged in a certain roughly graded series with a structurally simple form at the beginning and a structurally complex form at the end (for example, amoeba to amphioxus) or a structurally complex form at the origin and a structurally simple form at the end (for example, form the antenna of a nematocerous dipteron to the antenna of a Muscid).

It is clear, therefore, that when he speaks of a "natural classification", the systematist cannot really mean, a classification based on phylogeny or relationship by descent. Nevertheless, it is equally clear that he means something more than a classification based on resemblances without distinction. This is evident from the very fact that he distinguishes between "natural" and "artificial" classifications: as when he says that a grouping of flowers on colour is artificial, while a grouping on certain structural characters is natural.

It appears that in the last analysis the idea underlying the word "natural" is that of *necessity* or as indicating a relationship between *entities* or *unities* where the properties designated as specific are not linked by chance, but solidly attached one to the other or, better, emanate from some unitary principle. The recognition and description of such entities and of their relationships as entities is the objective of systematics. The principle involved here is therefore comparable to that invoked in the classifications of the mathematical forms.

The question then is, how does the systematist select the characters linked by a necessity? The only answer seems to be that he does so by taking permanence or constancy of pattern as the sign of necessity. The greater the number of elements involved in this pattern, the more peculiarly specific, from a morphological standpoint, the elements composing it, the more certain the systematist will feel that his material is *correctly* classified or that his classification is a true or natural one. Moreover in some cases, the characters used to define a systematic category may not merely form a constant pattern but may be clearly linked by functional necessity. The carnivorous or aquatic habits are not, in themselves, satisfactory systematic indices since they may have quite different morphological foundations; but when functional coordination and detailed morphological similarity coincide, the coordination itself strengthens the evidence from the morphological pattern.

For this reason, I feel myself strongly impelled to say that that some of the categories established for the Tachinid groups on adult characters are unnatural as compared with those that can be defined with reference to reproductive habit and larval forms; or, if they are natural, are demonstrated to be such by the evidence of the larvae and reproductive systems, rather than by the adult characters themselves. When a category is based on such an apparently slight character as the vestiture of the propleuron, this feeling is strengthened.

However, possession of flat plano-convex eggs containing undeveloped larvae and deposited on the body of the host, striking and characteristic though it is, is certainly not acceptable as the basis of a systematic category for it occurs not only in *Exorista* Meig. (=*Tachina* R.D.) and others of the Phorocerini of Mesnil, but also in the Phasiine flies, where the adult morphological pattern is strikingly different. Moreover, there are groups in which the larval morphology as we know it at present, is at once too indefinite and too variable to provide definite leads.

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[2] In a number of quarters this is now recognized. In the introduction to his great monograph on the American moths of the sub-family Phycitinae (U.S. Nat. Mus. Bull. 207, 1956) the late Carl Heinrich, after stating that he had hoped "to explore the phylogeny of the family" says that he finally realized it would be "a vain and futile performance".

"We don't know", he concluded, "what a primitive phycited was like. We don't know which forms evolved from which, or how. We weren't there. We may surmise; but the guess of one ignoramus is as good as another, and there is nothing to be gained, from either."

Thomas Borgmeier in his important work on neotropical ants ("Die Wanderameisen der Neotropischen Region" (1955)) has many pertinent remarks on this subject. "Die Systematik", he says "ist unabhaengig von Deszendenzgedanken". . . . ."Die Systematik ist Wissenschaft; Phylogenie ist eine Hypothese und kann deshalb nie die Grundlage einer Wissenschaft sein"—and he quotes Walther Horn: "Aus der aphyletischen Einstellung kann niemals ein Nachteil fuer die Systematik resultieren"—which is precisely the thesis I am examining in this paper.

Generally speaking, my impression is that it is probably not possible to break down the Tachinids on adult characters into groups that coincide with those defined on reproductive habit and larval characters. If, therefore, the adult groups are accepted as natural, and the larval groups also, we have a system which is apparently internally contradictory; but this contradiction can be resolved if we accept the analyses of Cuvier and Schiaparelli, regarding the system as "multidimensional", so that although it is a basic unity, yet owing to the number and character of the determining factors or parameters, it is not a simple linear arrangement, but a net or framework.

To understand the implications of Schiaparelli's interpretation of organic taxonomy, we must grasp a rather peculiar, but very important point: which is, that for him the taxonomic network has its factual origin in what we can only call a net-work of *real possibilities*. It does not result from an unrestricted modification of some basic living substance under the influence of chance. It exists in a sense *a priori* or rather potentially, as water exists potentially in hydrogen and oxygen; and its basic elements appear independently when environmental conditions permit. Also, while H_2O and a few other waters exist potentially in the universe, the entity HO_{10} does not exist potentially. The potentialities are real but limited.

From this it follows that at one point in time the available material may constitute only part of the taxonomic system that is really possible. It will therefore appear to us as the "torn net". Furthermore, a particular type may appear, subsist for a time, then disappear, but come again into existence at a later date and at some far distant point in space. Dollo's principle: that evolution is irreversible, therefore need not be accepted; and in many cases it is unnecessary to formulate hypotheses about land bridges to explain the existence of similar types in regions far removed one from the other. You will remember the zoologist who said that whole continents are raised up to prevent a marsupial from wetting his feet. Here again there is an idea expressed by D'Arcy Thompson, for example, with regard to the forms of the Protozoa and the evolution of the Ammonities. The basic principle is that physical laws determine what types are possible and impose certain limits on them.

In regard to the internal structure of the taxonomic system, Schiaparelli has also some interesting deductions. Assuming that its structure is as he defines it and because of the complex interrelations which result, we may expect certain consequences. One is the existence of gradations in the form of some organ existing in a particular type. This would not seem to be connected with the evolutionary hypothesis, since we find it in the inorganic world—for example with respect to the atomic weights of the elements or the physical state of the elements of the Fluorine-Iodine group at ordinary temperatures.

Given the structure of the system we may also expect, owing to the existence of a common parameter or determinant in several series, to find parallel series of gradations. Examples would be the series we can describe in the Dipterous families of the Stratiomyidae, Asilidae and Bombyliidae, with a progressive reduction in antennal size and structure or in the venation of the wings. For a similar reason we may find, in genetically separate types, some striking common feature. Schiaparelli cites the various races of domestic animals which have a large white zone around the body. An example in the insect world is the case of the white-banded bee, *Xylocopa inconstans*, and the Asilid, *Hyperechia bifasciata*. This has been interpreted as a case of mimicry produced by natural selection, although it does not appear that the Asilid, which is supposed to be the mimic, is in any need of protection. The Tachinids *Gymnochaeta* and *Chrysotachina* share with the *Lucilias* their green metallic colour. Many similar examples will occur to you. These resemblances—or what we so interpret,—exist here and now because certain physico-chemical processes produce them and there is, in the view of Schiaparelli, no need to speculate further about their origin, and particularly no need to invoke a fictitious history as an actual cause.

To points distant in the analogical series, there will correspond very different types. Nevertheless, in spite of the great difference in form they will have something in common. From this there may result a kind of bizarre incongruity or an unusual combination of characters, such as we find in *Hesperornis* and *Ichthyornis*, the toothed birds of the cretaceous deposits or *Archaeopteryx* of the jurassic, or, again the present-day serpents having two very small legs near the head. Such cases, Schiaparelli would say, are too rare to support the hypothesis of an evolution by gradual transitions but they appear in his interpretation, as results of the taxonomic order which are not less natural because they are unusual. Another example would be *Peripatus*, as peculiar in its distribution as it is in its structure. From this viewpoint, also, as I have said we can understand the apparent discordance we may observe, between the morphological affinities of adult and larval forms. It is usual to explain such facts by the hypothesis of evolutionary convergence but in the system of Schiaparelli this hypothesis is quite superfluous. We cannot of course positively disprove the suggestion that in many cases structural similarities are signs of genetic connection; but there are many facts that should inspire caution, one of which is the eye of the Cephalopods, which as you know presents an astounding resemblance to the eye of a Vertebrate, though there can be no genetic connection.

The homologies of anatomical parts, which according to the usual view is a proof of descent from a common ancestor are, in the interpretation of Schiaparelli, primarily and above all, evidence of systematic connection such as we observe in a family of curves or in elements of the same group. Since they are not necessarily produced by a genetic process, we have no obligation to say that they are evidence of it.

The interpretation of Schiaparelli with respect to the taxonomic system is of course quite foreign to our mental habits and probably most biologists who have heard of it have discussed it as a mathematician's fantasy. The first question that will be asked is of course, what has become of evolution in this system? Schiaparelli, it is true, describes his theory as one of evolution by fixed types or regulated evolution. However, he explicitly rejected the idea of specific transformations, saying that species are absolutely invariable in their characters. What occurs, if I understand him correctly, is a passage of matter through categories of a preordained system which is called preordained, simply because it represents what is really permissible under the laws which govern the universe; but this passage—which might but need not have a genetic character—would not necessarily, by any means, lead from the lower to the higher or from the simple to the complex. This also, Schiaparelli rejected. I do not really know, he said, whether the types of the Laurentian or lower Cambrian systems are each the simplest possible in its particular group but if they are, then this is merely because the environmental conditions would not permit of the existence of more complex forms. The higher categories were then, as the lower categories are now, *real potentialities*, for the realisation of which no real evolutionary development was required. He added, that individuals or groups of individuals might transform but the coordinated mutation necessary would clearly be no easier than a spontaneous generation, since nothing in the theory provides a preparation for the change and the sense of the theory is that an individual can live only as a manifestation of its specific type. However, this difficulty, to my mind, exists, exactly to the same degree, in all the current theories which do not, in my opinion, provide an acceptable explanation of the origin of the taxonomic system.

The same thing must be said about another weakness of Schiaparelli's theory, to be found in his view of correlations. For him correlation simply means a coexistence dependent on a basic formula or law. He did not think of it as functional or adaptive. Adaptive correlations therefore were no problem for him.

However for both Lamarckian and Darwinian evolutionists the genesis of adaptations has always been the major problem and it is because Darwin persuaded biologists that he had solved it, that his theory was so successful. The correlation that exists in a mathematical entity is real, but it depends on a kind of necessity different from the necessity in functional correlation which relates to the possibility of life in a real material entity composed of parts, which must cooperate to the same end.

For the Darwinians, adaptive coordination is in the last analysis, the result of chance. For many biologists this is an unacceptable proposition and so I find it. I feel that I am in good company, since the difficulty has been clearly recognized by such eminent biologists as Maurice Caullery (1948) and Emile Guyénot (1947). But if the theory of Schiaparelli is also unsatisfying, this is merely because, by substituting mathematical and material correlation for adaptive correlation, it simply purports to perform in an instant, the feat for which the Darwinians demand long ages, without making it more possible. Furthermore, the theory of Schiaparelli fails to distinguish between the specific unity and correlation in a complex, but non-living chemical compound and the specific unity and correlation in an organism, which exhibits something the non-living unit does not: namely a power of active adaptation, with respect to which the morphological or purely material correlations, while not negligible, are of secondary importance. In a word, I feel that Schiaparelli has thrown light on the nature of the taxonomic system and presents a much more objective picture of it than does the evolutionary philosophy. He has shown also that when the system of fixed types is properly understood it is seen to explain many points that are currently regarded as intelligible only in terms of evolutionary theory and are, for this reason regarded as arguments for it; but has not enabled us to comprehend the origin of the taxonomic system.

It would not be correct to say that Schiaparelli refused to accept the possibility of organic transformations. He nowhere claims to prove that the types of which he speaks originated independently. Indeed he explicitly allows the possibility of genetic connections. He does not clearly explain just what this might involve but would seem to have envisaged a process of coordinated and radical mutations, in other words a macroevolution. But the real interest of Schiaparelli's work is not in these familiar but unverifiable speculations. It is in his demonstration that a system of fixed morphological types not genetically connected, may exhibit the morphological peculiarities that are currently regarded as explicable only on evolutionary or phylogenetic principles. Though it passed unrecognized by his contemporaries, it was an important contribution to the criticism of evolutionary evidences, now long overdue, now developing in many quarters, still opposed by contemporary orthodoxy, but urgently necessary for the reestablishment of biology on an objective basis.

REFERENCES

Aldrich, J. M., and R. T. Webber. 1924. The North American species of parasitic flies belonging to the genus *Phorocera* and other allied genera. *Proc. U.S. Nat. Mus.* 63: 1–90.

Blackwelder, R.E., and A. Boyden. 1952. The nature of systematics. *Systematic Zoology* 1: 1.

Caullery, M. 1948. Génétique et Hérédité. *Presses Universitaires de France*, Paris.

Coquillet, D. W. 1897. Revision of the Tachinidae of America north of Mexico. *U.S. Dept. Agr., Div. Ent., Tech. Bull.* 7.

Curran, C. H. 1934. The families and genera of North American Diptera. *The Ballou Press*, New York.

Dobzhansky, T. 1951. Genetics and the origin of species. *Columbia University Press*, New York.

Grassé, P. P. 1938. Une controverse sur l'évolution. Rev. trimestrielle de l'éncylopédie francaise. *Librairie Larousse*, Paris.

Guyénot, E. 1947. L'origine des espèces. *Presses Universitaires de France*, Paris.

Horn, W. 1928. The future of insect taxonomy. *Trans. 4th Internat. Congr. Ent.*, Ithaca, 2: 34–51.

Mesnil, L. 1939. Essai sur les Tachinaires. *Imprimerie Nationale*, Paris.

Mesnil, L. 1944. *In* Lindner's Die Fliegen der palaearktischen Region. Lief. 153, 64g: 1–48. *E. Schweizerbart'sche Verlagsbuchhandlung*, Stuttgart.

Radl, E. 1930. The history of biological theories. *Oxford University Press.*

Schiaparelli, G. V. 1898. Studio comparativo tra le forme organiche naturali e le forme geometriche pure. Biblioteca—scientifico—litteraria. *Ulrico Hoepli*, Milan.

Schiner, J. R. 1862. Fauna Austriaca. Die Fliegen. I. *Carl Gerold's Sohn*, Vienna.

Sellers, W. F. 1943. The nearctic species of parasitic flies belonging to *Zenillia* and allied genera. *Proc. U.S. Nat. Mus.* 93: 1–108.

Snodgrass, R. E. 1951. Comparative studies on the head of mandibulate arthropods. *Comstock Publishing Co.*, Ithaca, N.Y.

Townsend, C. H. T. 1936. Manual of myiology. Pt. IV. *Charles Townsend & Filhos*, Itaquaquecetuba, Sao Paulo, Brazil.

Thompson, D'Arcy W. 1942. Growth and form. *Cambridge University Press.*

Williston, S. W. 1908. Manual of North American Diptera. *J. T. Hathaway*, New Haven.

Le Phylloxéra de la Vigne
Quelques Faits biologiques et les Problèmes qu'ils Soulèvent

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Je pense qu'aucun de mes auditeurs ne contestera l'éminente position qu'occupe la France parmi les pays producteurs de vin. Nos Bourgogne, notre Champagne, nos Bordeaux sont mondialement connus et appréciés. Et pourtant, depuis plusieurs décades, la viticulture française se trouve dans un grand marasme. Le "problème viticole", comme on l'appelle, est devenu l'une des préoccupations majeures de nos gouvernements, l'un des problèmes les plus disputés et discutés parmi nos concitoyens.

Eh bien, si ce problème existe, nous le devons principalement au *Phylloxéra de la Vigne.*

Mais, je me permettrai, avant d'aborder directement la question du Phylloxéra, de vous rappeler quelques notions historiques, ampélographiques et entomologiques. Elles sont nécessaires pour la suite de mon exposé.

HISTORIQUE

I—LE VIGNOBLE MONDIAL

A l'heure actuelle, 43 pays se partagent la superficie du vignoble, qui s'élève à 8.991.000 ha en 1955, avec une production de vin de l'ordre de 220 millions d'hectolitres. Je surprendrai probablement plus d'un délégué en vous apprenant que le pays qui nous accueille aujourd'hui d'une manière si hospitalière possède lui-même depuis quelques années un vignoble de 8.600 ha et consacre à l'amélioration de son encépagement des millions de dollars par an. Si je signale ce fait, c'est qu'il me paraît significatif. N'en déplaise à nos aimables hôtes, une telle extension mondiale du vignoble qui s'implante chaque année davantage dans des pays de tradition non viticole alarme à juste titre les économistes du problème et les derniers Congrès Internationaux de la Vigne et du Vin multiplient leurs adjurations et leurs recommandations aux gouvernements intéressés pour calmer ce que l'un d'eux a osé appeler "la folie mondiale des plantations".

Et pourtant, nous sommes encore, sur le plan mondial en pleine invasion, en pleine crise phylloxérique.

II—INVASION PHYLLOXÉRIQUE

En France, depuis 1880, nous avons vu en trente ans tout notre vignoble de vigne française (on appelle vignes françaises ou vignes européennes toutes les diverses variétés de *Vitis vinifera* Linné, par opposition aux autres vignes dites vignes américaines, comprenant plusieurs véritables espèces, *Vitis riparia, Vitis rupestris,* etc. . .) nous avons donc vu tout notre vignoble, plus de 2.500.000 ha, dépérir par l'invasion phylloxérique. Ce fut le plus grand désastre agricole que la France ait subi dans son histoire. Mais, si nous avons trouvé le remède au mal catastrophique en greffant nos vignes françaises sur les vignes sauvages américaines, nous n'avons pas résolu par là même le problème phylloxérique. Nous avons composé avec l'Insecte. Il en fut d'ailleurs de même dans les autres pays où l'invasion phylloxérique a revêtu et revêt encore divers aspects suivant les latitudes. C'est ainsi que l'on pourrait ranger dans le même type que celui de la France les vignobles d'Espagne et du Portugal, c'est-à-dire, les pays où l'invasion fut totale et le vignoble entièrement ravagé. D'autres pays comme l'Italie ont vu l'invasion s'étendre sur tout leur territoire sans amener cependant la destruction totale du vignoble, qui garde encore une bonne proportion de *Vitis vinifera* non greffé. Puis, des pays comme la Grèce, l'Allemagne et l'Australie, ont été ou sont encore partiellement envahis et espèrent, à grand renfort de lois draconniennes et parfois de lutte directe, maintenir le statu quo actuel ou du moins contrôler la reconstitution de leurs vignobles et éviter le désastre économique français des environs de 1900. Enfin, des pays comme Chypre et le Chili ou l'Iran sont jusqu'ici parvenus à rester hors de portée de l'Insecte, mais vivent désormais dans la crainte perpétuelle de le voir s'implanter dans leurs vignobles.

Ce bref tour d'horizon vous permet dès lors de mieux saisir l'importance du problème sur le plan international. Mais il serait temps désormais d'aborder l'aspect purement biologique de ce problème, sa complexité, les faits nouveaux sur la question, et les différentes solutions trouvées ou proposées par les diverses écoles qui l'ont étudié.

III—Les etapes dans la connaissance de la biologie du Phylloxéra

La France ayant été l'un des premiers pays touchés par l'invasion phylloxérique, il est normal de trouver dans les premiers chercheurs qui se sont intéressés à la question une équipe française de laquelle se détachent sans conteste les noms de E. G. Balbiani (1874 à 1884) et M. Cornu (1873 à 1878). A ces noms, les classiques de la littérature phylloxérique, s'ajoutent ceux de J. E. Planchon, J. Lichtenstein, V. Mayet, L. F. Henneguy, P. Boiteau et autres, et aussi ceux de l'Anglais J. O. Westwood, de l'Américain C. V. Riley, des Suisses V. Fatio, Demole-Ador, Schneider-Orelli, de l'Allemand Blankerhorn, du Portugais Graels, pour n'en nommer que quelques-uns.

Une deuxième période de recherche sur le Phylloxéra se place au début du 20ième siècle, avec les travaux parallèles et souvent concurrents de l'école italienne de B. Grassi et de l'école allemande de C. Borner. Grassi et Borner ont, chacun de leur côté, éclairé en partie quelques-unes des obscurités qui entouraient encore la biologie de l'Insecte. Le nom de Grassi brille d'un éclat tout particulier parmi ceux des biologistes qui se sont intéressés au Phylloxéra.

IV—Connaissances actuelles sur le cycle phylloxérique

Il me serait trop long d'évoquer en détail les étapes de la connaissance de ce cycle, classique entre tous. Chacun sait que de l'oeuf d'hiver pondu sous les écorces à l'automne naît une fondatrice gallicole qui, par parthénogénèse, redonne soit des jeunes dits gallicoles-gallicoles qui repiquent la feuille, soit des jeunes dits gallicoles-radicicoles qui descendent aux racines et donnent eux-mêmes par parthénogénèse des générations radicicoles. Parmi ces insectes vivant sur les racines, certains sous des conditions que nous préciserons plus loin, acquièrent des caractères nymphaux et, sortant du sol, se transforment en ailés. De ces ailés sortent les sexués, mâles et femelles. Cette dernière, après copulation, pond un oeuf unique, dit oeuf d'hiver, oeuf qui rentre en diapause pour éclore au printemps suivant.

Telles sont, très rapidement esquissées, les diverses phases du cycle. Il vous sera, dès lors, plus facile de suivre le développement de mon exposé. Et je me propose tout d'abord de vous parler des problèmes théoriques liés au cycle, pour envisager ensuite les voies nouvelles qui s'offrent à nous dans la lutte contre le Phylloxéra.

PREMIÈRE PARTIE : LES PROBLÈMES THÉORIQUES SUR LE CYCLE

I—Les problèmes biologiques soulevés par le gallicole

A—La présence ou l'absence du gallicole dans un vignoble

Il est assez commun de dire que la vigne française (*Vitis vinifera*), à l'inverse des vignes américaines, ne porte pas de galles. Et on conclut un peu trop hâtivement que les cycles du Phylloxéra diffèrent suivant les espèces de vignes. C'est une vue un peu sommaire. Du point de vue historique, rappelons-nous que c'est sur la vigne française, et par la phase gallicole, que fut constatée l'invasion phylloxérique. Par contre, aux Eyzies, lieu où nous travaillons en France, jamais une vigne américaine ou un hybride Franco-Américain ne nous a permis d'obtenir des galles spontanées, des galles de fondatrice. Il n'y a donc pas lieu de conclure d'une manière catégorique à l'existence de deux cycles distincts. On est donc conduit à examiner de plus près l'influence des facteurs externes et internes intervenant dans ce problème.

(a) Les facteurs écologiques

Ils sont capitaux. Dans beaucoup de pays ou d'endroits, la phase gallicole n'existe pas, *parce que les facteurs externes, climatiques en particulier, interviennent pour empêcher son apparition ou son développement.* Il y a *rupture* du cycle phylloxérique à différents stades. En effet, le gallicole dépend non seulement de l'éclosion de *l'oeuf d'hiver*, mais encore de l'existence même de cet oeuf, donc de sa ponte par le *sexué* qui est conditionné lui-même par l'existence de l'*ailé*, lui-même dépendant de la nymphose . . . . . En 1950, au VI° Congrès International de la Vigne et du Vin, Frézal souligne que, dans les régions sèches, ensoleillées et chaudes de l'Algérie, l'essaimage des radicicoles est contrarié. L'absence du gallicole dans ces régions s'expliquerait donc par l'absence d'humidité nécessaire à la nymphose proprement dite. Au même congrès, A. J. Winckler, délégué américain, souligne que l'unique et important facteur qui ait ralenti la propagation du Phylloxéra en Californie est l'absence des ailés. Nous-même, en France, aux Eyzies, nous avons pu montrer qu'à cent mètres de distance, mais de distance *verticale*, le cycle phylloxérique pouvait être différent sur des vignes identiques. Absence de gallicoles dans la vallée, cycle complet sur le plateau la dominant. En étudiant de plus près les facteurs intervenant, nous avons pu mettre en évidence que les basses températures nocturnes enregistrées dans la vallée, à l'époque de la nymphose (juillet, août, septembre) (nymphose qui s'y effectue néanmoins normalement), bloquent le développement des sexés qui n'arrivent pas à faire leur mue et donc à pondre l'oeuf d'hiver. Au contraire, sur le plateau dominant la vallée, où l'amplitude de température est nettement plus faible (de 3 à 4° en moyenne), les sexués évoluent normalement et l'oeuf d'hiver pondu éclot au printemps suivant. Nous avons pu ainsi établir le seuil biologique du Phylloxéra *sexué*. Le même phénomène semble jouer pour l'Allemagne, pays dans lequel Vigne et Phylloxéra vivent à leurs limites biologiques naturelles.

(b) Les facteurs internes

L'importance des facteurs externes ne doit pas cependant nous faire oublier, ou perdre de vue, la non moins grande importance des facteurs internes. Dans des vignobles où voisinent diverses espèces de vignes, hybrides ou américaines, donc toutes théoriquement réceptives au gallicole, il est curieux de constater par exemple que sur certaines seulement, et régulièrement chaque année sur les mêmes, on retrouve des populations gallicoles, tandis que sur d'autres on note l'absence non moins régulière des galles.

D'autre part, tout pépiniériste ou viticulteur peut constater qu'en serre *Vitis vinifera* est beaucoup plus réceptif au gallicole qu'en plein champ. Le métabolisme de la plante hôte et de son parasite sont profondément modifiés par les procédés de culture. C'est par l'étude de ces problèmes, et principalement des facteurs *biochimiques* que l'on doit trouver la solution aux anomalies du cycle ou à des différences inattendues dans des vignobles jouissant d'un même climat. Parmi les derniers travaux parus sur l'influence des facteurs internes et principalement des facteurs biochimiques, nous signalerons tout particulièrement ceux de J. J. Prince (Moscou, 1950). Nous aurons l'occasion d'y revenir, lors de l'étude des facteurs de résistance au Phylloxéra.

B—Le gallicole direct

Le cycle ordinaire du Phylloxéra est, nous l'avons vu: radicicole, ailé, sexué, gallicole. Mais peut-on passer directement du radicicole au gallicole, indépendamment des phases ailées et sexuées.

C'est le problème du "gallicole direct". Plusieurs auteurs l'ont étudié, et résolu expérimentalement dans des *serres*. En atmosphère très humide et chaude, ils ont pu assister à l'infection des feuilles par la montée des jeunes radicicoles le long du cep. Mais les données morphologiques et la distinction entre néogallicoles et néoradicicoles étant encore imparfaitement connues ou non admises par les expérimentateurs, diminuent la valeur des résultats enregistrés par ceux-ci. Cornu (1878), Balbiani (1874), Franceschini (1891), Borner (1910), etc. . . ont noté de tels faits. Le mérite d'une étude plus complète revient à A. Foà (1914) qui, tenant compte des nouvelles données acquises par l'école de son Maître Grassi, a jeté quelque lumière sur cet important problème. Nous mêmes, au cours de nos expériences sur le Phylloxéra, avons pu constater plusieurs fois la montée des jeunes radicicoles sur le cep pour aller donner directement des galles sur les jeunes feuilles. Mais nos observations et expériences étant faites dans des conditions particulières nous pensions que, dans la nature, un tel phénomène devait rarement se produire lorsque, dernièrement, au cours d'un voyage en Allemagne, un entretien avec le Dr Stellwaag nous apportait des documents nouveaux sur le problème: Le jeune Phylloxéra pique toujours la feuille à peine éclose de son bourgeon, car la feuille a un pouvoir de cécidogénèse très court. Dès qu'elle atteint une certaine taille, elle ne semble plus capable de réagir aux piqûres de l'Insecte en formant une galle. Au printemps, les galles des fondatrices, qui éclosent à l'époque du débourrement de la vigne, ne se trouvent de ce fait que sur les premières feuilles du cep (de la 1ère à la 6ème, ordinairement). Mais, entre l'éclosion de la fondatrice et celle de ses filles, il s'écoule près de 3 semaines pendant lesquelles le cep pousse vigoureusement, si bien que les galles de la 1ère génération ne se trouvent ordinairement qu'à partir de la onzième feuille. Dans un vignoble donc, on constate en règle générale une absence complète de galles sur les feuilles 7, 8, 9, 10. Tel est le schéma ordinaire d'implantation des galles sur les feuilles. Le Dr Stellwaag à qui nous exposions cette observation nous a montré des schémas totalement différents, où dès le départ de la pousse on constate une formation massive de galles, sans la solution de continuité du schéma classique. Et, sous réserve d'une étude morphologique de ces jeunes gallicoles, nous sommes d'accord avec lui pour expliquer ce phénomène par la sortie de jeunes radicicoles sous des influences dont le déterminisme nous échappe encore. En Allemagne, il se pourrait donc que la formation de galles toujours très rares soit due en partie aux gallicoles directs.

II—Sur quelques problèmes posés par la lignée hypogée

Comme le gallicole, le radicicole passe par 5 stades successifs, avant de devenir adulte. Les générations radicicoles se succèdent sans interruption du printemps à l'automne. On peut en compter 6 ou 7 et leur nombre est étroitement lié aux conditions atmosphériques. Si l'automne est doux, on trouve des adultes en train de pondre jusqu'en novembre. Cependant, dès octobre, on peut trouver certaines années des *hibernants* (jeunes radicicoles subissant la diapause hivernale) et ceci après seulement quelques jours de froid. A partir de la 2ème génération, c'est-à-dire dès la fin du mois de juillet, on distingue certains insectes du 3ème stade plus allongés que d'autres. Ce sont les prénymphes. A la mue suivante, apparaissent les fourreaux alaires: ce sont les nymphes.

A—Le problème des nymphes, nymphales et nymphoïdes

Les nymphes sont des radicicoles du 4ième stade et, comme telles, elles n'ont pas encore d'ouverture génitale, laquelle n'apparaît qu'au 5ième stade.

Si on examine le rapport $\frac{\text{N (Nymphes)}}{\text{Nymphes} + \text{Radicicoles}}$ en % (statistiques établies sur des vignes hybrides et des porte-greffes), au cours de l'été 1955, on constate que, du 1er au 15 juillet, il n'y a pas de nymphes—du 15 au 30, il y a 16% de nymphes—du 1er au 15 août, 54%—du 15 au 30, 55%—du 1er au 15 septembre, 37%—du 15 au 30 septembre, 9%. On peut en conclure que la nymphose a lieu principalement au cours du mois d'août et qu'elle intéresse un peu plus de la moitié de la population phylloxérique radicicole. Mais il y a de grandes variations individuelles, en rapport non seulement avec les diverses espèces de vignes, mais encore avec les ceps à l'intérieur d'une même espèce, avec les lieux et les années. On constate néanmoins que pour chaque cep il y a une période très nette où le nombre des nymphes l'emporte de beaucoup sur celui des radicicoles. Nous en avons quelques exemples sur des porte-greffes, en particulier 3306 (hybride *V. riparia* x *V. rupestris*) où nous avons pu constater un essaimage intéressant plus de 92% de la population phylloxérique radicicole. Sur ces vignes, il est donc juste de parler de ce que l'on a pu appeler la "purge" annuelle des hybrides et des porte-greffes.

A côté des nymphes typiques qui, irrévocablement, se transforment en ailés, on rencontre des phylloxéras intermédiaires entre la nymphe et le radicicole, c'est-à-dire, des individus au corps trapu, arrondi (comme le radicicole) mais à fourreaux alaires et à ommatidies (comme la nymphe). Ce sont ces intermédiaires que Grassi et son école ont appelés "ninfali" et que, par similitude, nous appelons "nymphales". Mais, parmi ces fausses nymphes, il en est indubitablement du 5ième stade, c'est-à-dire des adultes reconnaissables à leur pore génital. Ce sont des insectes nés d'une nymphale, ainsi que nous avons pu le constater. Pour les distinguer de ces dernières, nous nous proposons de les appeler des *nymphoïdes*. La mue qui les fait passer du stade *nymphal* au stade *nymphoïde* est une mue *régressive*. La régression porte sur les caractères morphologiques typiques: ommatidies (nombre et forme), longueur et forme des antennes, longueur des fourreaux alaires, etc. . ., réduction de la puissance des muscles thoraciques. Biologiquement, ces nymphoïdes pondent des oeufs donnant des radicicoles normaux.

Cette mue régressive, qui rappelle par certains côtés celle qui existe chez les Termites, est sans doute liée à un changement dans l'activité des glandes endocrines. Mais, les individus sujets à cette régression sont exceptionnels et leur place dans le cycle phylloxérique a beaucoup moins d'importance que celle de leurs homologues chez les Termites.

B—Les différences entre populations phylloxériques hypogées des diverses espèces de vigne et les conséquences qui en résultent

Les *hibernants* s'observent en grand nombre sous l'écorce radiculaire de *Vitis vinifera.* Ils sont beaucoup moins nombreux sur les *vignes américaines* ou les *hybrides.* Les *nymphes*, d'autre part, sont moins abondantes sur la vigne française que sur les vignes américaines. Ces différences de population phylloxérique selon les espèces végétales ont une répercussion profonde sur le comportement de ces dernières à l'égard des attaques de l'Insecte. En effet, le départ massif des nymphes réduit chaque automne, dans une large mesure, la population phylloxérique des vignes américaines. D'autre part, l'absence presque totale d'hibernants sur les vignes américaines fait qu'au printemps suivant leur système radiculaire a le temps de se reformer et de croître avant la migration vers les racines des jeunes néogallicoles-radicicoles. Sur la vigne française, au contraire, les nombreux hibernants des grosses racines (leur lieu d'élection) déterminent des lésions irréparables et multiples qui empêchent la montée de la sève au printemps. Ce sont les tubérosités, beaucoup plus nocives que les nodosités (piqûres des radicelles). De plus, dès le printemps, lors du *débourrement*, ces vignes sont envahies par les hibernants qui se réveillent et détruisent immédiatement les jeunes radicelles d'un plant déjà affaibli par les tubérosités. Le plant français (*Vitis vinifera*) ira en s'affaiblissant d'année en année. L'hybride ou la vigne américaine, au contraire, à chaque printemps, reformera son système radiculaire avant les grandes invasions phylloxériques de l'été. L'infection peut se maintenir d'année en année sans que le plant en souffre beaucoup.

En outre, il existe entre les deux types de vigne des différences importantes dans la réaction aux piqûres du Phylloxéra. Les tubérosités des troncs radiculaires déterminent des nécroses profondes dans les tissus de *Vitis vinifera*, nécroses qui altèrent l'écorce, la couche génératrice et même les rayons médullaires. Il se forme des "bouchons" sur le passage de la sève. Sur les vignes américaines, au contraire, seule la couche corticale, non vitale, est atteinte. L'assise génératrice reste ordinairement intacte et le passage de la sève continue. Mêmes différences en ce qui concerne les nodosités des radicelles: une nodosité se produisant sur la Vigne française détermine en quelques jours la mort de la radicelle. Sur la Vigne américaine, où la croissance est plus rapide, et où les tissus sont moins altérés par la piqûre, la radicelle continue à pousser, mais ne meurt généralement pas. La jeune racine forme une série de zig-zags, courbures déterminées par les piqûres, mais la circulation de la sève continuant, la racine alimente toujours la plante.

Dans l'explication des phénomènes de résistance des Vignes américaines au Phylloxéra, on doit donc tenir compte non seulement des *facteurs propres à ces vignes* (croissance plus rapide des racines, résistance des tissus, etc. . .) mais aussi des *facteurs biologiques propres au parasite* (rareté d'hibernants et nymphose plus abondante). L'hôte et le parasite y jouent chacun leur rôle

III—Le complexe Phylloxéra-vigne

Vous n'avez pas été sans remarquer combien il est difficile de parler du Phylloxéra sans parler constamment des diverses espèces de vignes qui l'hébergent. C'est qu'en réalité s'instaure entre l'hôte et son parasite un véritable complexe biologique aux interférences multiples.

Des faits récents viennent confirmer par une voie différente cette notion de complexe. Les travaux de J. J. Prince (Moscou, 1950) jettent une lumière intéressante et nouvelle sur les relations Vigne-Phylloxéra.

L'auteur soviétique a remarqué que la sève puisée par le Phylloxéra contient des fragments de matières protéiques. Quand le tissu est piqué, un enzyme protéolytique est libéré par le Phylloxéra, enzyme qui appartient vraisemblablement au groupe des cathepsines. A l'aide de ce ferment, le Phylloxéra hydrolyse le cytoplasme des cellules piquées et transforme les protéines en matériaux assimilables pour lui. Mais, la cathepsine n'est efficace que dans un milieu à faible rH, tandis qu'elle devient inactive pour des valeurs élevées de ce même potentiel oxydo-réducteur.

Et c'est ici qu'interviendraient les différences notables entre vignes résistantes et vignes sensibles. Dans les vignes résistantes (vignes américaines), le protoplasme a un rH élevé, de sorte que les matières albuminoïdes ne sont pas décomposées par l'enzyme de désintégration produit par le Phylloxéra. Ce dernier retire donc ses soies rostrales et cherche ailleurs sa nourriture. Dans les vignes sensibles, au contraire, (*Vitis vinifera*), la cathepsine décompose les matières protéiques de la plante. Il y a désintégration du contenu cellulaire et mort de la cellule. Des substances d'oxydation et de réduction (oxydases, peroxydases, flavones, catalases) dont les proportions varieraient suivant les espèces de vignes, leur lieu d'origine (feuilles, racines), interviendraient en outre pour activer ou retarder cette action de la cathepsine phylloxérique sur le protoplasme de la plante. Telles seraient, d'après l'auteur soviétique, les bases biochimiques de la résistance des différentes vignes envers le Phylloxéra.

Mais, il faudrait confronter ces vues avec les faits biologiques du Phylloxéra. Or, c'est sur sa plante originelle (vignes américaines) que le Phylloxéra s'est le mieux adapté. C'est sur elle qu'il effectue son cycle entier, qu'il a sa fécondité maximum (nombre d'ovarioles, nombre de générations plus élevés). *Vitis vinifera* n'est pour lui qu'un hôte de remplacement. Comment, dès lors, concilier ces faits biologiques avec les résultats biochimiques de notre collègue? Il y a là matière à discussion et c'est dans la symbiose de ces diverses disciplines que l'on doit trouver la solution de certains problèmes phylloxériques encore incomplètement résolus.

IV—Le problème des races de Phylloxéra

Parmi ceux-ci, le problème des races de Phylloxéra suscite encore des controverses.

Le problème relatif à la pluralité des races de Phylloxéra a été posé en Allemagne. C. Börner, de 1910 à 1926 et même plus tard, a progressivement affirmé et développé la théorie qui porte son nom. La voici très brièvement résumée.

En 1910, il signale qu'en Lorraine, en serre, le Phylloxéra ailé préfère, pour y déposer ses oeufs, les vignes françaises aux vignes américaines, et que l'oeuf d'hiver ne se trouve que sur la vigne française et aussi sur *V. labrusca* (vigne américaine apparentée à *V. vinifera*); qui se chargent alors de galles. Il n'y a, par contre, pas de galles foliaires sur les vignes américaines qui en portent généralement le plus. Il croit donc que l'on peut distinguer ce Phylloxéra comme étant une race biologique spéciale qu'il nomme "*pervastatrix*". Puis, au cours des années suivantes, il distingue des races dites du Nord, et d'autres dites du Sud, d'après leur origine, et leur donne les noms de *Phylloxera vastatrix* et de *Phylloxera vitifoliae*. Entre ces deux races, il établit des différences de divers ordres: (a) *Différences morphologiques*, en particulier, dans la longueur des soies rostrales qui, d'après la corrélation a/b (a = longueur des soies, b = longueur du tibia de la 3ième paire de pattes) permettrait de séparer morphologiquement les deux races. Mais celles-ci se distinguent aussi par (b) *Différences biologiques* dans leurs attaques, soit des feuilles soit des racines. Réunissant toutes ses observations sur un très grand nombre de cépages, il propose une classification assez complexe des vignes, selon leur réceptivité gallicole ou radicicole à l'égard de l'une ou l'autre race. Vignes attaquables par les deux races—vignes jouissant de l'immunité à l'égard de la race *Vastatrix*—vignes jouissant de l'immunité à l'égard de la race *Vitifoliae*, etc. . . En résumé, Borner affirme qu'il existe deux races au moins de Phylloxéras: races géographiques, morphologiques et biologiques. Tel est le postulat de Börner, postulat très sévèrement critiqué par l'école italienne de Grassi en particulier, et par de nombreux autres chercheurs, mais admis ou confirmé par diverses équipes surtout d'Europe orientale et d' U.S.S.R.

Si la théorie de Börner a connu une telle notoriété, c'est moins croyons-nous par l'intérêt théorique d'une mise en évidence de diverses races de Phylloxéras, que par les incidences pratiques énormes qu'elle a entraînées. Suivant les directives de Börner, en effet, toute une partie de la recherche viticole mondiale s'est orientée vers une recherche *génétique* de vignes *immunes* à la race la plus nocive, voire aux deux races. (On appelle *vignes immunes* des vignes où le parasite ne peut se développer normalement). Börner, en effet, avait laissé entrevoir un tel espoir aux généticiens. D'autres chercheurs, sans se soucier du problème théorique posé par Börner, nièrent ses extrapolations sur le plan pratique et cherchèrent plutôt à créer des cépages *résistants* (c'est-à-dire, tolérant le parasite) qu'à créer des cépages immuns.

Nous avons essayé de mettre en évidence de telles races en France. Nous n'y avons pas réussi. Nous avons montré la fragilité des critères morphologiques de différenciation fondés sur la longueur des soies rostrales. Ces critères varient non seulement suivant les générations phylloxériques, gallicoles ou radicicoles, mais encore *suivant les cépages et même les ceps;* nous avons également parlé précédemment dans cet exposé des différences biologiques du comportement phylloxérique dans une même région, sous l'influence des facteurs écologiques et ceci indépendamment de toute question de races. Un récent voyage d'information dans les régions viticoles d'Allemagne nous a fait comprendre en outre que la querelle Grassi-Börner enregistrant de part et d'autre des résultats contradictoires avec du matériel identique échangé entre eux n'était et ne pouvait être qu'un *dialogue de sourds.* En effet, en Allemagne, la sexualité dans le cycle phylloxérique est quasi inconnue. Depuis de nombreuses années, le Phylloxéra se perpétue par parthénogénèse indéfinie, purement radicicole. Rien d'étonnant, *a priori*, que dans de telles conditions, des races se soient diversifiées. C'est un phénomène banal chez beaucoup d'Hémiptères. D'autre part, la discontinuité du vignoble allemand, dont l'importance dans la marche lente de l'invasion phylloxérique est si grande, et les conditions de limite biologique dans l'établissement de tels vignobles permettent une explication plausible de phénomènes aberrants pour des conditions plus normales réalisées par les vignobles italien ou français. En France, où le Phylloxéra pullule, gallicole et radicicole, surtout depuis l'implantation des hybrides, il n'y a, à notre avis, ni *problème théorique ni problème pratique* de "race". Tous les biotypes, races, variétés, s'il y en a, sont tellement mêlés, croisés, hybridés, que nous nous trouvons en face d'*un seul et même Phylloxéra qui ne pose qu'un seul et même problème*: trouver des vignes qui n'en meurent pas.

DEUXIÈME PARTIE: LES PROBLÈMES THÉORIQUES LIÉS À LA LUTTE CONTRE LE PHYLLOXÉRA

L'importance des recherches concernant le Phylloxéra réside, en effet, non seulement dans l'étude fondamentale du cycle, un des plus complexes parmi les Aphides, mais encore dans la recherche appliquée de vignes résistantes aux attaques de l'Insecte. Cette recherche appliquée au Phylloxéra fait d'ailleurs partie d'un ensemble de recherches viticoles comprenant l'étude de la résistance aux maladies cryptogamiques et aux attaques de parasites, et aussi l'étude plus difficile de l'amélioration *qualitative* du vignoble. Des facteurs économiques importants, nationaux et internationaux entrent en jeu et souvent passionnent un débat qui devrait d'abord se discuter sur un plan plus théorique. C'est à cet aspect du problème que nous nous attacherons, et plus particulièrement à la résistance des vignes au Phylloxéra.

Devant l'invasion phylloxérique et la nécessité de maintenir un vignoble productif, les premières solutions proposées furent des solutions immédiatement rentables. En France, après de multiples essais de lutte directe, rendus inefficaces par la vitesse de l'invasion, on recourut au système du greffage (greffon français sur pieds américains). Le système du greffage a deux avantages: 1°) Il permet de maintenir un vignoble productif malgré la présence du parasite. 2°) Il garde intacts les facteurs de la production primitive (cépage, sol) et assure ainsi la pérennité des caractéristiques du produit livré au consommateur.

Mais, il a ses inconvénients: coût élevé de la reconstitution des vignobles, problèmes nouveaux posés par l'affinité greffon-sujet, mauvaise résistance des feuilles de *vinifera* aux maladies cryptogamiques, etc. . .

On doit donc le considérer comme un palliatif provisoire et rechercher d'autres solutions.

Une de celles qui viennent naturellement à l'esprit est la *solution génétique: création de vignes franc de pied qui ne meurent pas sous les attaques du parasite.*

Mais il y a deux manières de vivre: *vivre avec son mal* (recherches de producteurs directs *résistants*) ou *vivre sans maladie* (recherches de vignes *immunes*).

I—La solution de "l'immunité"

Elle est née en Allemagne, pensons-nous, en filiation directe avec la théorie de Börner; puisque le ou les Phylloxéras adoptaient tel ou tel mode de vie, suivant les espèces de vignes en présence, on devait parvenir à créer des vignes immunes à l'une ou l'autre race, ou mieux encore aux deux races. C'était l'espoir final de Börner. Cette théorie a suscité en Allemagne de nombreux travaux et continue à orienter encore certains laboratoires. On a cependant, si nos renseignements sont exacts, abandonné l'idée de créer des vignes entièrement réfractaires aux parasites. L'idéal serait donc aujourd'hui de parvenir à créer des porte-greffes indemnes de la race la plus nocive pour le vignoble allemand. Si l'on entrevoit immédiatement les avantages d'un tel système (plus de soucis pour les problèmes de “résistance” des vignes au Phylloxéra, possibilité de créer des vignobles localisés *sans* Phylloxéra), on aperçoit aussi les faiblesses d'une telle orientation. Elle a pour base un postulat sévèrement critiqué par plusieurs écoles (la théorie des “races” de Phylloxéras): si même on l'admet pour des régions limitées comme l'Allemagne où le cycle reste hypogé, donc aberrant, la portée de tels travaux ne peut donc être que *locale*, et les résultats ne peuvent s'appliquer aux pays où le Phylloxéra retrouve sa sexualité normale et mélange ses gènes multiples (la France méridionale, par exemple). C'est pour l'avoir bien compris qu'en Allemagne même d'autres écoles ont pris une autre orientation.

II—La solution génétique des vignes résistantes

S'il ne s'agissait que de créer des vignes résistantes, le problème serait simple, puisque ces vignes existent pratiquement parmi les espèces américaines. Par la sélection et la génétique, le problème serait vite résolu. Mais, il s'agit de produire du vin et du *vin de qualité*, qualité jusqu'ici donnée par le seul *Vitis vinifera*. (Nous ne parlons ici que de la *qualité* liée au cépage. La notion “de qualité” est évidemment beaucoup plus complexe. La qualité d'un vin a pour facteurs non seulement l'*encépagement* (choix du cépage) mais encore les *conditions écologiques* (sol, exposition, climat, etc. . .) et aussi les *facteurs oenologiques* (procédés de vinification)).

La question préalable à laquelle on doit répondre en premier lieu est la suivante: *Peut-on rassembler dans une même cépage les facteurs de qualité et les facteurs de résistance au Phylloxéra et aux maladies cryptogamiques?*

La plupart des nations ont immédiatement répondu “non” en interdisant l'hybride, croisement entre *V. vinifera* et espèces américaines, postulant à priori que toute amélioration de la qualité ne pouvait se faire qu'à l'intérieur de l'espèce *V. vinifera* dut-on se contenter du palliatif du greffage comme un pis-aller en matière de lutte contre le Phylloxéra. Mais, d'autres nations, ne négligeant pas à priori l'augmentation de résistance due aux vignes américaines, ont étudié scientifiquement le problème. Nous nous devons de vous faire part, entre autres, des résultats obtenus en Italie par *Pirovano* et en Allemagne par *Husfeld*.

A—Apport de Pirovano sur la résistance au Phylloxéra de *Vitis vinifera*

Tous les Italiens connaissent les obtentions Pirovano dans le domaine du raisin de table. Le succès de l'“Italia” par exemple, (métissage Bicane x Muscat de Hambourg) a dépassé le cadre national et ce nouveau produit est désormais connu et apprécié dans le monde entier. Ces résultats pratiques remarquables dérivent de croisements judicieusement faits et s'appuient naturellement sur les lois de la génétique. Ils ont permis, entre autres, de lever un voile sur les caractères de résistance de *Vitis vinifera* au Phylloxéra de la Vigne. Cherchant à créer une variété précoce de raisin de table, Pirovano prit pour géniteurs, d'une part le cépage “Grec blanc” (ou Grecanico, Bellone, Tabacca. . .) qui s'était montré dans certaines localités et sous certaines conditions de terrain particulièrement résistant au Phylloxéra, et d'autre part le cépage “*Précoce d'Ischia*” à fruit noir, à grains petits, avec un aspect de vigne sauvage, rustique, peu productif. Un semis effectué en 1904 donna plusieurs exemplaires, mais fut envahi par le Phylloxéra. Seul, survécut un plant qui prit le N° 17 dans le catalogue de sélection. Ce fut le point de départ de recherches génétiques sur la résistance au Phylloxéra. En autofécondation des N° 17, on constate en FI qu'un quart de la population présente des caractères de résistance, mais aussi des caractères de petitesse dans les grappes et les raisins. Cette corrélation se confirme malheureusement en F2 et Pirovano en conclue que *la recherche de la résistance phylloxérique dans la vigne européenne donne des résultats exactement contraires à ceux attendus pour l'amélioration qualitative des raisins.* L'utilisation possible de ces *vinifera* résistants serait seulement souhaitable dans les cas de mauvaise affinité entre greffon *vinifera* et porte-greffe américain.

C'était en somme assez peu encourageant, mais il y avait là néanmoins des prémices de travaux intéressants. Faut-il voir dans des raisons analogues l'abandon des travaux de même ordre commencés par les généticiens allemands et, en particulier, par l'Institut de

Recherches pour la sélection des vignes du Geilweilerhof (Pr. B. Husfeld), précédemment installé à Muncheberg, près de Berlin? Le fait est qu'actuellement l'Institut Allemand est nettement orienté vers la solution de l'*hybride*, c'est-à-dire, du croisement entre espèces différentes de vignes.

B—Apport du professeur B. Husfeld

L'Institut Allemand, sous l'impulsion de son Directeur, a effectué des milliers de semis, tant au Geilweilerhof qu'à Muncheberg, son premier lieu d'implantation. C'est près de 30 ans d'expérience qu'il nous livre donc déjà en ce domaine. La position actuelle de B. Husfeld est très catégorique. Il répond affirmativement à la question préalable, ce qui nous paraît très important, à savoir que toutes les qualités des vignes se combinent librement. Il est donc théoriquement possible, par les méthodes génétiques, d'arriver à créer des vignes qui allieraient aux facteurs de résistance des vignes sauvages américaines, les qualités organoleptiques de *Vitis vinifera*. Bien plus, le prof. Husfeld pense pouvoir affirmer, dans l'état actuel de ses recherches, que la *qualité* (qui est une notion très complexe comprenant sucre, alcool, acides, extraits, bouquet, etc. . .) est transmise héréditairement, non seulement par la vigne européenne, mais aussi par les vignes américaines. Cette qualité n'est que *masquée* dans le cas des vignes sauvages par des substances étrangères, par leur saveur et leur odeur (goût de fox et d'herbe, en particulier). On peut, par voie de suppression; en particulier, par des "*croisements en retour*", arriver à éliminer les mauvais caractères organoleptiques des vignes américaines.

En ce qui concerne les facteurs de résistance au Phylloxéra, le problème, d'après B. Husfeld, est un des moins compliqués. C'est un facteur "dominant" qui se transmet à 50% des obtentions.

Ajoutons que la valeur des tests de résistance qui président au choix des nouveaux types et à leur multiplication, soit comme géniteurs possibles, soit comme variétés culturales, permet un contrôle rigoureux et une amélioration constante de ces nouveaux types. C'est, à notre avis, *la seule voie possible de recherche en matière d'amélioration par croisement.*

Mais, qu'il nous soit possible, en retour, de soulever quelques objections contre la solution de l'hybride. L'hybride, solution à la crise phylloxérique et par extension à la crise viticole résoud peut-être certains problèmes, mais il en pose aussi de nouveaux: il remplace un produit traditionnel, le vin, *jus fermenté de Vitis vinifera*, par un nouveau produit. Ceci est très important et, malgré tous les artifices et les succès de la génétique, jamais un Château-Yquem, par exemple, ne pourra être obtenu par un hybride. Là-dessus, je crois que tout le monde sera d'accord. On pourra peut-être boire un jour prochain un vin dénommé Château-Yquem, comme on boit déjà des "Bourgogne" et des "Champagne" de tel et tel pays, mais seul le nom sera le même. *L'enfant n'aura plus le même père.* L'hybride donc ne sera, s'il l'est un jour, qu'une solution limitée, à moins qu'un processus irréversible ne nous fasse abandonner nos grands crus. Avouons que ce serait un beau passé qui disparaîtrait.

Mais, l'entomologiste qui s'intéresse au Phylloxéra prévoit dans son domaine des objections sérieuses à la solution de l'hybride.

1°) Pas plus que le greffage, il ne résoud le problème. Puisque la vigne continue à vivre avec son parasite. Bien mieux, on le multiplie, puisque l'hybride réceptif au gallicole augmente la population phylloxérique gallicole et radicicole du vignoble? Nous ne le constatons, hélas, que trop en France.

2°) La résistance d'un cépage au Phylloxéra a peut-être (sûrement même) des bases *génétiques*, mais aussi dépend énormément des conditions *écologiques*. Les exemples abondent; souvenons-nous des premiers essais espagnols désastreux avec les porte-greffes ou hybrides prétendus résistants (ils l'étaient en d'autres lieux). Stellwaag a montré d'autre part, dernièrement, que la vitesse de la poussée radiculaire (dépendant du cépage, mais aussi des conditions de sol et de culture) jouait un rôle primordial dans la résistance des vignes. Une poussée rapide sauve la radicelle de la piqûre phylloxérique, une faible poussée entraîne la mort. Nous pourrions multiplier les exemples. Mais l'espace nous est limité.

Telles sont quelques-unes des objections que nous pouvons soulever.

L'économiste, de son côté, voit dans l'hybride une aggravation de la crise viticole; sur le plan français, mais déjà aussi sur le plan international, la surproduction est latente.

L'hybride, gros producteur, ne peut, ipso facto, qu'augmenter cette surproduction. Mais nous ne voulons pas nous étendre en ce domaine qui sort de notre compétence et du cadre que nous nous sommes fixé.

Messieurs, en conclusion, nous pensons que notre but serait atteint si vous sortiez de cette conférence convaincus que le problème phylloxérique reste un problème d'actualité. Que rien, sinon une meilleure mais non totale connaissance de l'Insecte, n'a été trouvé. Que nous ne devons pas nous endormir dans la fausse sécurité du greffage ou de l'hybride. L'échéance phylloxérique est encore devant nous. De nouvelles menaces surgissent du fait même de la présence de l'Insecte dans nos vignobles, ou de sa venue prochaine. Sans parler des nouvelles maladies de la vigne, je veux dire, des maladies à virus, problèmes angoissants pour les agronomes du moment. Problèmes où la part du Phylloxéra, encore indécise, pourrait devenir quelque jour prochain prépondérante.

Restons donc vigilants. Le Phylloxéra est un danger permanent, qui doit nous tenir en haleine et continuer à susciter l'émulation des divers chercheurs dans les pays de vignobles.

The Content of the Science of Ecology from the Standpoint of an Entomologist

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Ecology is a term which means different things to different people. Yet it is convenient to have if not a completely watertight definition at least a general agreement on the main objects of the ecologist. It is especially fitting to deal with this subject before an audience of entomologists since all applied entomology is essentially a branch of ecology when it is not chemistry. It is also appropriate on an occasion like the present plenary session, since so much excellent ecology of the type which agrees best with the definition which I am going to propose is being done in Canada.

Ecology is concerned with the size and manner of distribution of populations of living organisms. Taxonomists may be interested in geographical distribution but they are not much concerned with the size of or with the fluctuations in the populations of a species. Physiologists may be interested in the way the structure or the behaviour of an animal leads to a particular type of distribution but not as a rule in the size of the population. From the ecologists' point of view, the pattern of distribution both on the large and the small scale must be known before the population can be measured in any satisfactory way.

We have recently had what amounts to a new textbook of Ecology in Andrewartha and Birch's book "The distribution and abundance of animals". I suspect, however, that the title conceals an important fallacy. The authors in their first chapter attempt to show that distribution and numbers are really different aspects of the same thing. They claim that ecologists attempt to account for the abundance of species in particular places and that since the character of the place (or habitat) determines the local level of abundance, therefore the distribution pattern and the level of abundance are due essentially to the same causes. I do not believe that this is generally true though it becomes more and more nearly so as one approaches the periphery of the whole area of distribution. In the large central area to which the species is best suited the factors which determine the population level in any one year may be largely independent of those that determine the distribution of the species.

We can surely see this if we take the very familiar example of a caterpillar which feeds on a single species of plant. The distribution of the species will then be limited entirely by the food-plant in the part of the range where the climate is favourable. In most years, however, it will be factors other than the food-plant which determine population-density in the areas where the species occurs. It is possible that numbers and distribution would be associated more closely if we averaged density over all areas, including the patches in which the species was absent, but this procedure would be artificial.

One does not learn very much about an organism merely by listing the elements of which it is composed. One has to study processes and it is best and often necessary to study the simplest ones first. In the same way, in ecology, a list of the species of animals which live together in a locality is not of much use, except to a limited extent, to the taxonomist or zoogeographer. One has rather to study processes—the ways in which population levels are controlled. Clearly the start of such a programme must be a single species and the factors which influence it. The other organisms are brought in as they are shown to have an effect on the prime object of study. Other animals come in most obviously as parasites or predator though less direct effects are quite common. Those acting through the vegetation are frequent and the influence of species which provide an alternate food for predators may be considerable.

The chief points seem to be, first not to assume that species affect one another but to prove it; second, to measure these effects as accurately as possible. The second point is fundamental, apart from anything else, for one over-riding reason. The interrelations between an animal population, climate and the other concurrent organisms are of the type which can only be sorted out, in the short run, by some form of multivariate analysis. This is because the factors all interact with one another as well as with the dependent variate. There is in fact no completely independent variable for even climatic factors which are uninfluenced by insects all influence one another. Multivariate analysis is only possible if the factors have all been measured in numerical terms. I must add that I am not suggesting that multivariate analysis will provide a theory of population-balance which will be valid for several consecutive generations but it may tell one what has happened in any particular year.

There seem, in fact, to be short-term and long-term methods of investigating population problems. The former are concerned with short-period deviations from an approximately steady state, including under this term the regular seasonal curve of abundance shown by any particular instar in temperate climates. For investigating these, the methods of multivariate analysis seem to be the most powerful, though as with all statistical tools they only provide valid conclusions if used with biological insight and when supported by experiments.

The longer term problem concerns the steady state itself which is still very difficult to investigate under field conditions. It is probably determined by relating long term changes in the balance of reproduction and mortality, usually of more than one species. Multiplication by reproduction, particularly over more than one generation, leads to relations which multivariate analysis is unlikely to disentangle.

Two forms of uncertainty arise in ecological work. The fundamental one was indicated many years ago by W. R. Thompson as having close analogies with the uncertainty principle in physics. You cannot investigate an animal population without interfering with it but if you interfere with it, it is not the same as it was before. The usual necessary interference is the removal of samples, but frequent sampling may lead to damage to the habitat. Usually, the more you wish to know about the population and the greater the accuracy of your estimates, the greater the interference. This can only be partially avoided in very large uniform habitats, if such exist.

The other type of uncertainty has a more practical basis but may prove to be more important in the end. The more species are shown to be interrelated in the dynamics of a population the less it is possible to investigate any one of them adequately. Frequent population estimates, measurements of reproductive rates, mortality, movements, etc., can only be made simultaneously in a relatively small number of species. Theoretically, more could be done by a larger team, but, apart from other difficulties, this might lead to too much interference with the population or the habitat. In general, if a large number of species has to be studied, the information obtained about any one of them will tend to be less precise and more qualitative, less quantitative.

The greatest difficulty at the moment is to make any quantitative estimate of the effects of predators but a number of workers are now trying to develop new methods which will enable us to do this. The most hopeful seems to be to use the methods of serology to determine what predators have been eating. This has already been done in Canada and is now being developed in Britain also.

Ecology is a subject with many side-lines and bye-ways, many of which are important in particular problems, but I believe the subject can only be given general coherence if the study of population-dynamics is regarded as its central thread.

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SYSTEMATICS

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By Donald T. Ries
Illinois State Normal University
Normal, Ill.

Characters of Value in the Classification of the Aleyrodidae

By Louise M. Russell
Ent. Res. Br., U.S.D.A.
Washington, D.C.

Speciation: The Center and the Periphery

By William L. Brown, Jr.
Harvard University,
Cambridge, Mass.

ABSTRACT

The current models of geographic speciation are held to be inadequate to explain the rise of generally-adapted species, from which originate most of the higher categories. A new model is suggested to account for the formation of such potent species. It is thought that new genetic types arise mostly in the center of the species, and are carried outward in general by emigratory movements of the populations involved under pressure of intermittent density increases. This process gives rise to a central-peripheral pattern of geographical variation for generally-adaptive characters; a few probable examples are cited from the literature. Geographical contact is lost between central and peripheral-refugial populations when the total population of the species, or a large segment of it, suffers a decline and retreat to the most favorable breeding areas. The isolation thus achieved, and subsequent expansion phases, are the break-and-make of contacts required by classical population taxonomy. If renewed contact occurs after successful development of reproductive isolation, character displacement and geographical displacement may be important agencies in furthering specific differentiation between central and peripheral elements. It is considered that this hypothesis supports, and is supported by, the theories of geographical distribution put forward by P. J. Darlington.

INTRODUCTION

Modern systematics rests on the assumption that species normally arise when the parent populations are somehow split into geographical fractions. The fractions must remain apart long enough to allow reproductive isolation to develop between them. The idea of geographical speciation still stands as the most reasonable general hypothesis, despite arguments from many sides. For most zoologists who have thought in terms of population systematics, however, the concept of geographical isolation seems to have been limited to the consideration of only two models, which I think we can conveniently call *division* and *colonization.*

In *division*, the parent population is split by the intrusion of a physical or biotic barrier, such as a glacier, a desert, the arm of a sea, a mountain range, and so on. The process is essentially a passive one.

In *colonization*, the parent population is surrounded by a barrier, such as the ocean, that is normally impassable to the species. However, rarely a propagule does succeed in crossing the barrier and settling new territory. The parent and colonial populations are thus isolated, perhaps indefinitely.

No doubt both of these kinds of isolation occur and are instrumental in producing new species. But I think that we should doubt that these simple types of isolation can account for the most important kind of species, by which I refer to those species that reach a high degree of general adaptedness, and which are therefore in the best position to give rise to new major taxonomic categories. In giving long thought to this matter of modes of geographic isolation, I have been led to consider a third possible model for speciation through geographical isolation. It seems to me that this model, stated in the form of a general hypothesis, may have promise in guiding and interpreting research relating to speciation, and especially to the formation of species at new generally-adaptive levels. Essentially, the hypothesis is a synthesis of facts and ideas current in two fields of study: population dynamics, and geographical variation, and by geographical variation I do not, of course, mean the mere proliferation of subspecies.

THE HYPOTHESIS[1]

The maximum geographical range attained by a species over an indefinite period of time includes areas favorable and also some unfavorable for its continuous breeding and increase. Within the maximum range, the populations of the species normally undergo successive

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[1] The hypothesis dealt with in this article is substantially covered, with additional examples, in my article, "Centrifugal speciation". (Brown, 1957, *Quart. Rev. Biol.* 32: 247-277).

expansions into the less favorable peripheral areas, alternating with contractions into more favorable refuges. The expansions and contractions are the inevitable sequelæ of density fluctuations affecting all or part of the species at one time. The more important genetic changes tend to be incorporated in the central populations, and are carried outward with these during the phases of expansion. With the phases of contraction of the range, populations of the species disappear from the peripheral areas, except in the relatively restricted refugial pockets or islands that are favorable enough to allow survival of some expansion-phase remnants. At this stage, of course, the central populations are geographically isolated from the peripheral remnants, permitting the expected accumulation of genetic differences between them. If the differences between central and peripheral isolates mount to the point of reproductive isolation, the next phase of expansion can be expected to establish the geographical contact needed to confirm the relationship of the two entities as species.

The hypothesis is stated first in order to allow the reader to compare it as a whole with the analysis of each separate point. These analyses follow, forming the body of the paper. The sentences in italics are the parts of the hypothesis above, now isolated for discussion one at a time.

POINT 1. *The maximum geographical range attained by a species over an indefinite period of time includes areas favorable and also some unfavorable for its continuous breeding and increase.*

That this is so is evident to all, I think. Favorable areas vary in extent, but the biggest ones usually seem to be the most stable and to have the largest number of niches available. In such areas occur the populations that are densest and most continuously breeding, and therefore most likely to give rise to new generally-adaptive types of the kind likely to be superior under most environmental conditions met by the species. Unlike peripheral isolates, such relatively large and continuous or near-continuous populations are prevented from attaining the stricter modes of local environmental adaption by a high rate of genetic flux from several directions (see below, and Fig. 1).

We may term these large, favorable areas "evolutionary centers". Evolutionary centers are not necessarily equivalent to geographical centers of range, nor need they be stationary over long periods of time. It is obvious that the evolutionary center for many wide-ranging animal species of North America is the southeastern United States, but the species that occur there now cannot expand eastward because of the neighboring Atlantic Ocean. But where an evolutionary center occurs away from serious barriers, it is often more or less coincident with both the geographical center of the species range and with the center of the land mass on which it occurs, as in the cases of many species of tropical Africa and America.

POINT 2. *Within the maximum range, the populations of the species normally undergo successive expansions into the less favorable peripheral areas, alternating with contractions into more favorable refuges. The expansions and contractions are the inevitable sequelæ of density fluctuations affecting all or part of the species at one time.*

There is a fair amount of information on range expansions of various animal species, and a little on contractions. Writers on these subjects commonly link expansion to amelioration of climate, while retreats are often blamed on the activities of mankind. However, most accounts are anecdotal, and are entirely inadequate in their investigation of causality. The realization that this is the state of affairs has begun to dawn with the dissemination of the theories and arguments making up the science of population dynamics. More and more frequently, it is being found that density is linked to emigration, which is, after all, not unexpected from elementary considerations.

In general, it is now being found that animals emigrate from favorable to less favorable or distinctly unfavorable areas only when population density approaches or threatens to approach a critical stage with respect to some life requisite of the species, such as food or shelter. It is important to realize, as David Lack has shown so clearly, that the actual emigratory movement is often set off by proximate conditions, such as physical crowding or raised temperature, which are not in themselves a threat to the supply of requisites, but which often accompany or precede such a threat. These proximate conditions act to trigger reactions leading to emigration, and perhaps to maintain and direct movements once started, well before the density reaches the catastrophe point at which the affected populations exhaust a critical requisite.

We have apparent examples of this in the lemmings, and in birds like the crossbills, waxwings, lapland buntings, and others. Among the arthropods, there are poorly-studied cases among the collembola, the millipeds, and many insects. The migratory locusts and grasshoppers are better known.

Migratory Orthoptera generally have a fairly well defined center of dispersal, their permanent breeding ground, or outbreak area. When the hoppers are reduced to low densities, they are usually confined to these areas and show a sedentary kind of behavior. As density builds up, the behavior changes through successive generations, and mass emigration from the area is the final result. A few individuals always seem to be left behind to re-seed the outbreak area. There are also changes in form and color, constituting phases. The phases apparently act to fortify and direct the modal behavior pattern of the emigrant population, but their morphological components are not always well correlated with each other or with the behavior states of the insects. For these insects, the behavioral and phase changes amount to a mechanism, produced by more than one proximate environmental stimulus, which serves to divert a Malthusian crash. The surplus individuals are carried right out of the permanent breeding area, but their loss is not always a total one for the species. Emigrations involve at least some possibility of extending the species range, and they presumably also serve to spread new characters among the peripheral elements, thus constantly tending to improve the whole species (Key, 1950).

The California oak moth is another case of density-dependent emigration, both in larval and adult-female stages. It has been shown by Harville (1955) that this member of a tropical family (Dioptidæ) is able to extend its range at least temporarily in California, chiefly through the spreading of gravid females by the wind. The females tend to lay their eggs in the center tops of the host oak trees, but if the tree has already been badly defoliated, they will flutter off to search for another tree. They are weak fliers, so that if a proper host is not available, the very weakness of their flight makes them likely to be carried off for long distances by the wind. Something similar to this may occur in the pierid *Ascia monuste* (Chermock, 1946; Nielsen and Nielsen, 1950), although in this species, active emigratory flight is indicated, northward in southeastern North America, and southward in the Plata Basin at the southern edge of its range.

Various objections have been raised against the idea of density-reactive emigration, but to me none of these is very convincing. Two schools of thought exist concerning the importance of density-reactive factors in population processes, with workers like Nicholson (1954) and Lack (1954) on one side, and others, such as Andrewartha and Birch (1954) opposed to the general idea of density-conditioned emigration as a very significant feature of population dynamics. One of the chief points of confusion in population dynamics studies lies with the concept of competition, which often gets too far from the dictionary definition. The dictionary sticks pretty close to "together seek," but biological authors often tend to include the ideas of aggressive or interferent behavior by the members of one species or individual against others of their kind. In my opinion, interferent behavior is one (frequently stereotyped) means of avoiding competition, either within or between species. Other means of avoiding competition are divergent adaptation ("character displacement", see below) and geographical dispersal, one form of which is emigration. The important thing here is to recognize population density as a source of emigratory pressure when it is high; competition is the ultimate density homeostat.

POINT 3. *The more important genetic changes tend to be incorporated in the central populations, and are carried outward with these during the phases of expansion.*

The connection between the larger, favorable evolutionary centers and the probability that new generally-adapted types will arise there most frequently has been mentioned already. However, even though we grant an hypothetical species range of absolutely uniform favorability, inhabited by a population of absolutely uniform density—even then, it can be shown that adaptively superior genetic characters will arise more often near the geometric center of the range than at the periphery. And, as a corollary to this, it can be shown that such an ideal situation would involve a differentiation between a relatively heterogeneous central set of populations and a relatively homogeneous peripheral set. This situation is illustrated by the diagram (Fig. 1).

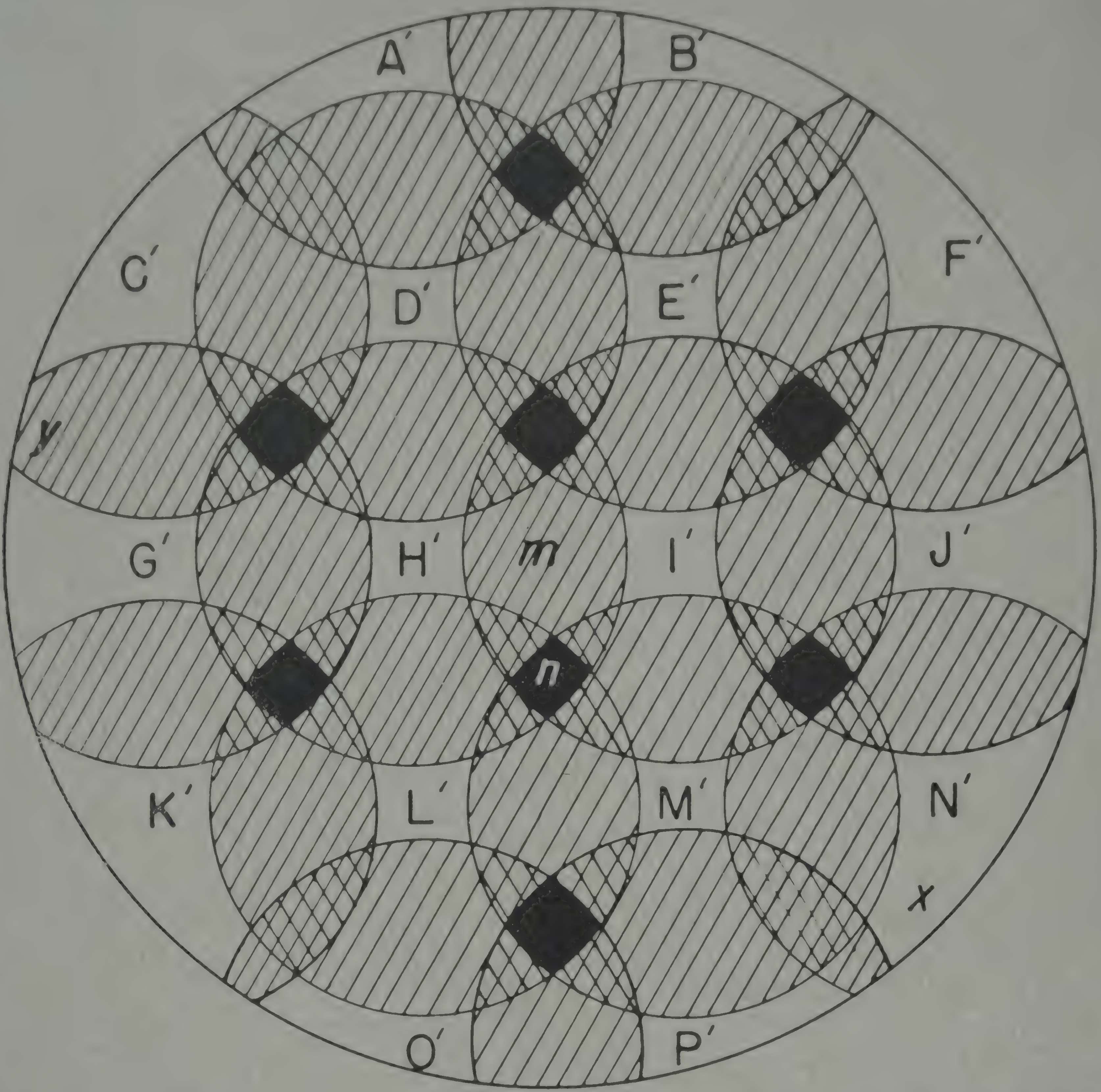

Fig. 1. Diagram illustrating central-peripheral differentiation in an ideally uniform species range. Explanation in text.

The large circle includes the uniformly favorable, uniformly populated range of the species as a whole. The smaller circles each represent a new, adaptively superior character, which because of its superiority is spreading through the population. These characters can be mutations, combinations, chromosomal readjustments, or any other sources of genetic change; it is up to population genetics to specify what kinds of genetic changes are represented in such a case, and to outline the details of their behavior. For us, they are simply new characters. Where two small circles overlap, we have two new characters differing from the "wild type" of the rest of the range. In this model, as many as four circles overlap at certain points, meaning that populations at such a point will carry four of the new characters. Now, it will be noticed that the periphery of the range has less overlapping of new-character circles, for the simple reason that no populations exist outside the range boundary to support a new character. Notice that given peripheral populations, as those at points *x* and *y* are more similar, that is, differ by fewer new characters, than are populations of the center, such as *n*, to much closer peripheral populations, such as *x*. By the use of character formulæ, it is easy to find the number of characters by which a population at a given point differs from one at any other point in the range. For example:

Population at point *x*, formula A B C D E F G H I J K L M N' O P
Population at point *m*, formula A B C D E F G H' I' J K L M N O P

Number of characters different between populations of the two points = 3.

From this diagram, our thoughts now turn naturally to the question of how this pattern of differentiation might apply to real species ranges, heterogeneous both in spread of habitats and in the corresponding densities of population. If the range tends to be distributed according to the favorable-center, unfavorable-periphery plan already discussed above, we might expect that the pattern of our diagram would not only hold good, but that it would in some respects be exaggerated. And if the pattern does hold good, then we should expect to find it in natural species populations. Do central-peripheral patterns of variation occur commonly in animal species? The answer is that it looks as though they might, although the evidence so far is hardly more than suggestive. We can't tell what the situation really is until more taxonomists get away from describing so-called subspecies and turn their attentions to the real study of geographical variation. Central-peripheral patterns are masked, rather than revealed, by the need of subspecies describers to find "diagnostic" characters; such characters are almost entirely limited to those features adaptive for specific localities, and approaching the "classic" racial distributional pattern. The entire emphasis on "diagnostic" characters sees the trait that does turn up in several remote parts of the range either ignored or "averaged in" with others. To make things worse, locally-adaptive characters often involve qualities that are all too conspicuous to the human taxonomist. Color, size, relative appendage length, rate of development—all are obvious locally- or areally-adaptive characters in many instances, and all are extensively utilized in describing animal races.

Characters without obvious adaptive significance from the local viewpoint may be extremely important from the general, but such characters are often obscure and difficult to study. A certain population of an insect species, for example, may have developed a short-cut in fat digestion, or an altered reproductive rate, that would be obscure to a taxonomist, but highly advantageous to any population of the insect to which it can manage to spread. Usually, we only begin to recognize such characters when, like resistance to chlorinated hydrocarbons, they begin to threaten our public health and agricultural plans.

Outside the insects, a very interesting example of the distribution of an obscure character, probably directly or indirectly generally-adaptive because it appears to be spreading in all directions, is the loss of the rudimentary oviduct in the male of the frog *Rana pipiens.* Figure 2 shows the distribution of populations with and without oviducts in the male. Oviductless frogs occupy the entire center of the North American portion of the range, and appear at a few points in peripheral regions otherwise held by populations with male oviducts. This appears to be the usual pattern shown by a spreading character. Other "diagnostic" characters, which run chiefly to north-south distinctions, show no concordance with this central-peripheral one. It should be noted that the distribution of the frogs with oviducts is peripheral without any obvious correlation with ecologies of the regions concerned.

Similar distribution, but with a different central area, is noted for the external vocal sac character in the same species (Moore, 1944). Other patterns related to this one are found among the drongos, genus *Dicrurus* (Vaurie, 1949); in the barn owl, *Tyto alba* (Voous, 1950); in Lepidoptera like *Melinæa lilis* (Forbes, 1927), and in the camel cricket *Ceuthophilus uhleri* (Hubbell, 1954).

Professor Bequaert (1931) has pointed out to me the color variation in the hornet, *Vespa crabro*, which in Britain and again in China and southeastern Asia has yellow occiput, whereas the intervening populations of Europe and Asia have brownish occiput. The population introduced into North America, now spreading rapidly, is from a continental European population with dark occiput.

One mechanism of spread is illustrated by the change from predominantly black to predominantly red phases of the imported fire ant, *Solenopsis sævissima* (Wilson, 1951, 1953) in the Gulf Coast area of the United States. In this area, the original native species of the same group appears to have been *S. xyloni*, which was replaced over much of its Gulf Coast range by an invasion of *S. geminata*, probably during historical times. As the third invading species, *S. sævissima* first appeared in Mobile, Alabama, probably introduced by commerce, about the time of World War I. The form appearing here was the black form, and this remained relatively stable until about 1930, when a reddish form of the species appeared in the Mobile population. Shortly thereafter, the whole population began to spread outward

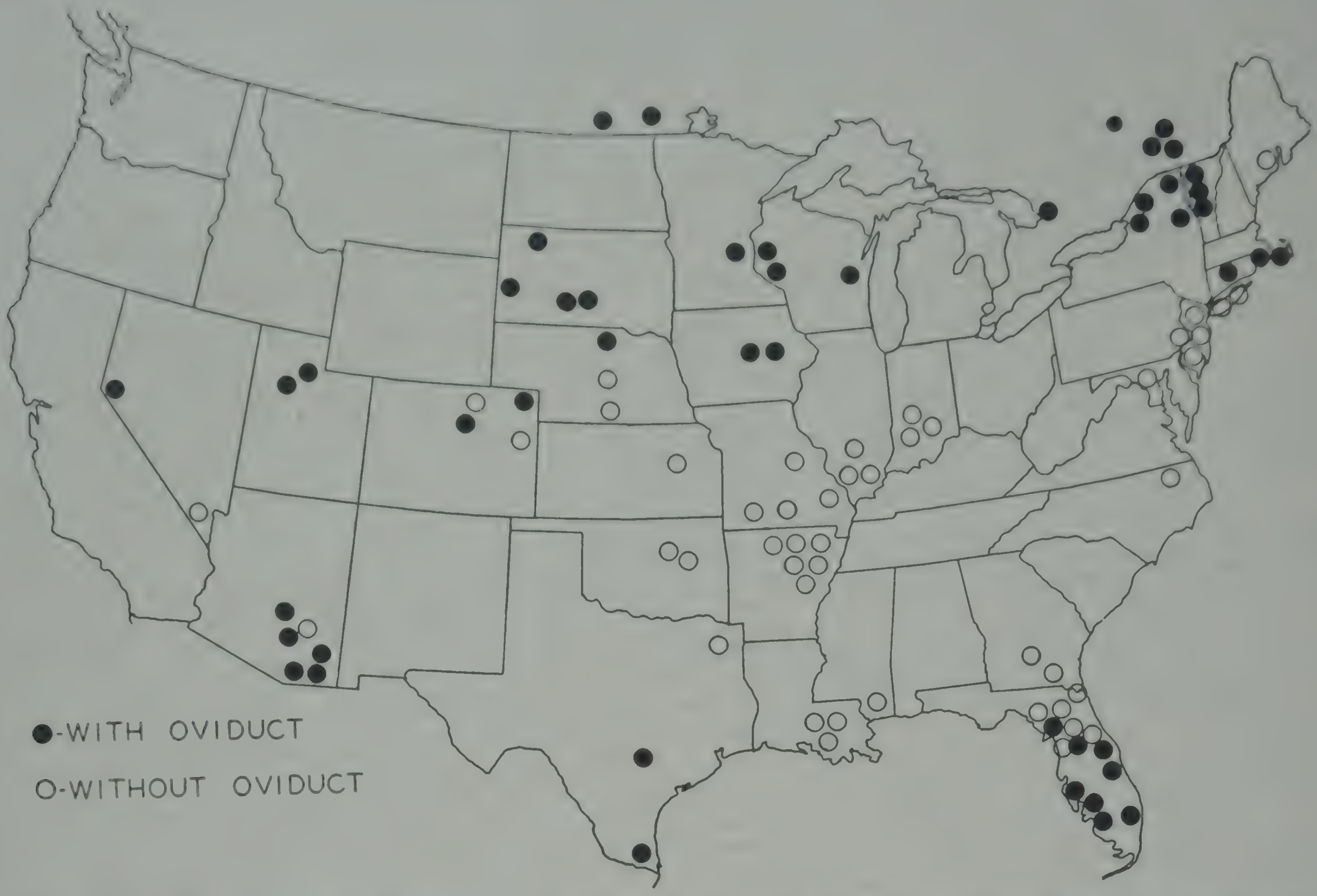

Fig. 2. Map showing the distribution of population samples of the frog *Rana pipiens* in which the males either have or lack rudimentary oviducts. (After Moore).

from Mobile into the surrounding country with great rapidity. From all appearances, the introduction of the red form into Mobile may have sparked the higher rate of spread.

Turning to the source area of the fire ant, Wilson found that the species *S. sævissima* ranges from the Amazon Basin, where the prevailing color is yellow, to northern Argentina, where the blackish form is predominant. The color changes from yellow to black through a cline running through shades of reddish, especially in southern Brazil and the Plata Basin. The importations obviously came from the southern parts of the range, the red form possibly representing a stock from among the clinal intermediates that was secondarily introduced into Mobile by commerce.

In the years between 1930 and 1949, the increase in the range of the fire ant in the Mobile area was most dramatic. Outlying colonies in neighboring states were seeded by transport through nursery stock and wind-borne females of the ant. Some of these colonies were pure black-phase, and some were intermediate or red in 1949. Only rather casual observations have been made since 1949, but we know that the main area of infestation has now spread outward and engulfed many of the outliers by 1955. Unfortunately, we do not know what changes have taken place in the color phase composition of these foci during recent years.

Within the main area of infestation, populations are frequently very dense, and in most areas overrun by the fire ant, the two other members of the group, *S. geminata* and *S. xyloni*, have been completely extirpated. This area is roughly circular, centered on Mobile. By 1949, the red forms had become clearly predominant over most of this area, especially in the central portions. Black populations existed mostly mixed with reds and intergrades between red and black, and, except for a few restricted pockets within the main range, the blacks were limited pretty much to peripheral parts of this range. Wilson visited one peripheral area again in 1956, and he tells me that the black form appears to be yielding ground to the red at this point, especially in the crucial stages of young and incipient nests. Most or all of such small nests he found were of red phases.

There is complete intergradation everywhere between the red and the black phases, and the picture is one of swamping of the black by the red form, both genetically and by direct warfare. War is constantly waged between adjacent nests of all phases in densely populated areas. This is an important case that should be followed up by further studies. It shows how in nature one character can replace another from the center of the range outward, creating some degree of central-peripheral differentiation. It is also interesting to note that the three very closely related species of this group appear to have had native ranges successively farther from the center of evolution presumed for this group. *S. xyloni* appears to have been entirely restricted to North America; *S. geminata* probably was limited to Mexico, Central and northern South America, and *S. sævissima* ranged southward in central South America. *S. geminata* was able to overrun the less arid parts of the range of *S. xyloni*, and was in turn successfully overrun by *S. sævissima* in much of this same territory.

According to Crampton (1932), the land snail *Partula vexillum* of the Pacific island of Moorea has twice alternated between sinistral and dextral population-types within a half century, and the changes appear to have moved in waves across the small island in the same direction and from about the same point of origin in a certain large valley.

The cases of central-peripheral variation listed above are only a part of those encountered in the literature and in conversations with specialists of different animal groups, but it would certainly be wrong to claim that clear-cut central-peripheral variation is a commonly reported phenomenon. In order to find out more about the frequency of this pattern, we need much more data. We may hope that much more attention will be given by taxonomists to the plotting of character variation for its own sake.

Thus far, we have considered cases in which the variation is confined to single species. Some of this variation doubtless can be related to ecological factors that, by fortuitous circumstances, have a central-peripheral distribution. But certainly not all such variation can be explained away in this manner. The cases of *Rana pipiens*, *Tyto alba* and the fire ant, in particular, suggest that generally-adaptive characters are in back of the visible variation.

POINT 4. *With the phases of contraction of the range, populations of the species disappear from the peripheral areas, except in the relatively restricted refugial pockets or islands that are favorable enough to allow survival of some expansion-phase remnants. At this stage, of course, the central populations are geographically isolated from the peripheral remnants, permitting the expected accumulation of genetic differences between them.*

I think that this process can be pretty much taken for granted, even though evidence for it is scanty in the literature. It follows from the facts of uneven ecological distribution within the range that during contraction periods, populations will survive differentially. It should be possible for readers to think of cases where disjunct populations occur beyond the main species boundary. Such populations may be likened to pools left by a receding tide. Populations that may be of this nature are known in the butterflies (*Ascia*, *Vanessa*), as well as in birds like the crossbill (see below). The expansion phase can be expected to increase the number of colonist propagules that successfully cross "permanent" barriers. Wandering birds and butterflies far at sea probably often highlight a high density situation in the permanent breeding range. Such wanderers are, of course, often potential colonists.

It seems likely that genetic differences building up between central and peripheral isolates will originate in both kinds of populations. Changes in peripheral populations thus isolated should tend to be local, simple adaptations to local environmental conditions. Central populations, for reasons already discussed, should originate more of the general kinds of adaptations, likely to be more complex and more subtle than are the peripheral specializations. Central changes should also be due less often to the effects of random fixation and gene loss, if these factors are indeed of importance in speciation processes.

POINT 5. *If the differences between central and peripheral isolates mount to the point of reproductive isolation, the next phase of expansion can be expected to establish the geographical contact needed to confirm the relationship of the two entities as species.*

Most expansions probably occur before reproductive isolation is complete, so that central populations overwhelm and swamp the peripheral ones, as in the case of the fire ant. If this is the common method of evolutionary progress of single species through geographical time, it may afford a method of accounting for what seem to be marked changes of evolutionary pace in some lineages. Another probability is that species arise frequently, but that peripheral ones are nearly always quickly wiped out by competition or interference from succeeding species-waves. Only a fraction of expansions can produce successful, selfmaintaining species pairs; otherwise, the number of species would be much greater than it is. Even so, the ever growing numbers of pairs or complexes of sibling or "cryptic" species becoming known to us is evidence that "trial species" may rise and fall much more frequently than we have thought heretofore. We ought to give more attention to the study of differences between the individuals making up successive density peaks; hardly anything is known about such variation with time in Recent animal species. Already, there are hints of changes from peak to peak in a British butterfly (Ford, 1945), and possibly also in North American *Melanoplus* plague grasshoppers.

If a great enough degree of reproductive isolation exists between newly-remet populations, the very fact of their sympatry or contiguity may be expected to force a further divergence of their form and behavior through character displacement. The phenomenon of character displacement has been dealt with more fully by Brown and Wilson (1956), and Dr. Wilson discusses it elsewhere in these Proceedings. Briefly, it may be said that character displacement is the divergence (morphological, behavioral, physiological, ecological) between two populations of animals living together or side by side, when the same two species are relatively convergent in areas where only one of the two occurs. Character displacement is probably brought about by two principal requirements: the need to avoid interspecific hybridization (gamete wastage), and the need to minimize the effects of competition for life requisites. We should expect to find cases of character displacement occurring on a central-peripheral basis where specific differentiation has already taken place, and a few possible cases are next discussed.

Finches of the Northern Hemisphere genus *Loxia*, known as crossbills, have crossing, somewhat asymmetrical bills used in opening the cones of conifers for seeds that form the staple of their diet. Heavier bills are best adapted for opening the tough, heavy cones of *Pinus;* the parrot crossbill (*L. pytyopsittacus*) of northern Europe has such a heavy bill in exaggerated form. Occurring with the parrot-like species, and also extending far beyond in Europe, Asia and North America, is a more slender-billed species, *L. curvirostra*, adapted to feeding on the more delicate spruce and fir cones. In Scotland, the Balearic Islands, North Africa, Cyprus, Crimea and other isolated points around the fringes of Europe, there are separate populations of crossbills with bills of intermediate thickness. These are often assumed to be races of *curvirostra*, but actually no one has produced binding evidence that any or all of these isolates do belong to either *curvirostra* or to *pytyopsittacus*, the pronunciamentoes of taxonomists of the group notwithstanding. The best that can be said for these isolates is that they appear to be undisplaced populations in a vast central-peripheral character displacement system. It is significant, I think, that the genus *Loxia* in general is noted for migratory and even irruptive mass movements that carry the birds far beyond their permanent breeding ranges, and surely must account for the isolated crossbill colonies in places like Hispaniola, Luzon and Annam. A flourishing colony was established in Ireland within historical times, spread widely through the country, and eventually became extinct there (Griscom, 1937).

Figure 3 shows the distribution of the four extremely similar sibling species of the *Drosophila pseudoobscura* group, a North American offshoot of the mainly Palæarctic *obscura* group (Dobzhansky and Epling, 1944). The heavy lines mark the range of *pseudoobscura*. The black area marks the *persimilis* range as estimated from the distribution of the round white dots within it, representing the actual records as of 1944. The white crosses mark the few records of *miranda*, and the single record of *frolovæ* is located at the point where the encircled letter "f" appears. Aside from being morphologically very similar, the three species occurring in California apparently have much the same habits and foods, so that some competition among them is probably inevitable. At some points, these three live in the same general localities, but their ecologies show average differences, especially in the altitudes at which optimum population sizes exist. *Pseudoobscura* is most often dominant at particular localities, though marked seasonal and year-to-year fluctuations in the sizes of *pseudoobscura* and *persimilis* are well known. *Miranda* is rare, local, and probably close to the primitive type, as shown by the arrangement of chromosome III. It is backed up to the coast and a few high altitude localities. *Pseudoobscura* and *persimilis* are highly polymorphic in III and Y chromosome types. The character displacement case referred to is in the Y chromosome, in which a certain type, called "type I," is found in most *persimilis* and in many *pseudoobscura* populations, but is not found in any of the latter where these are sympatric with *persimilis*, in the Pacific Coast States. It would certainly be interesting to know the adaptive correlations of this Y chromosome inversion type.

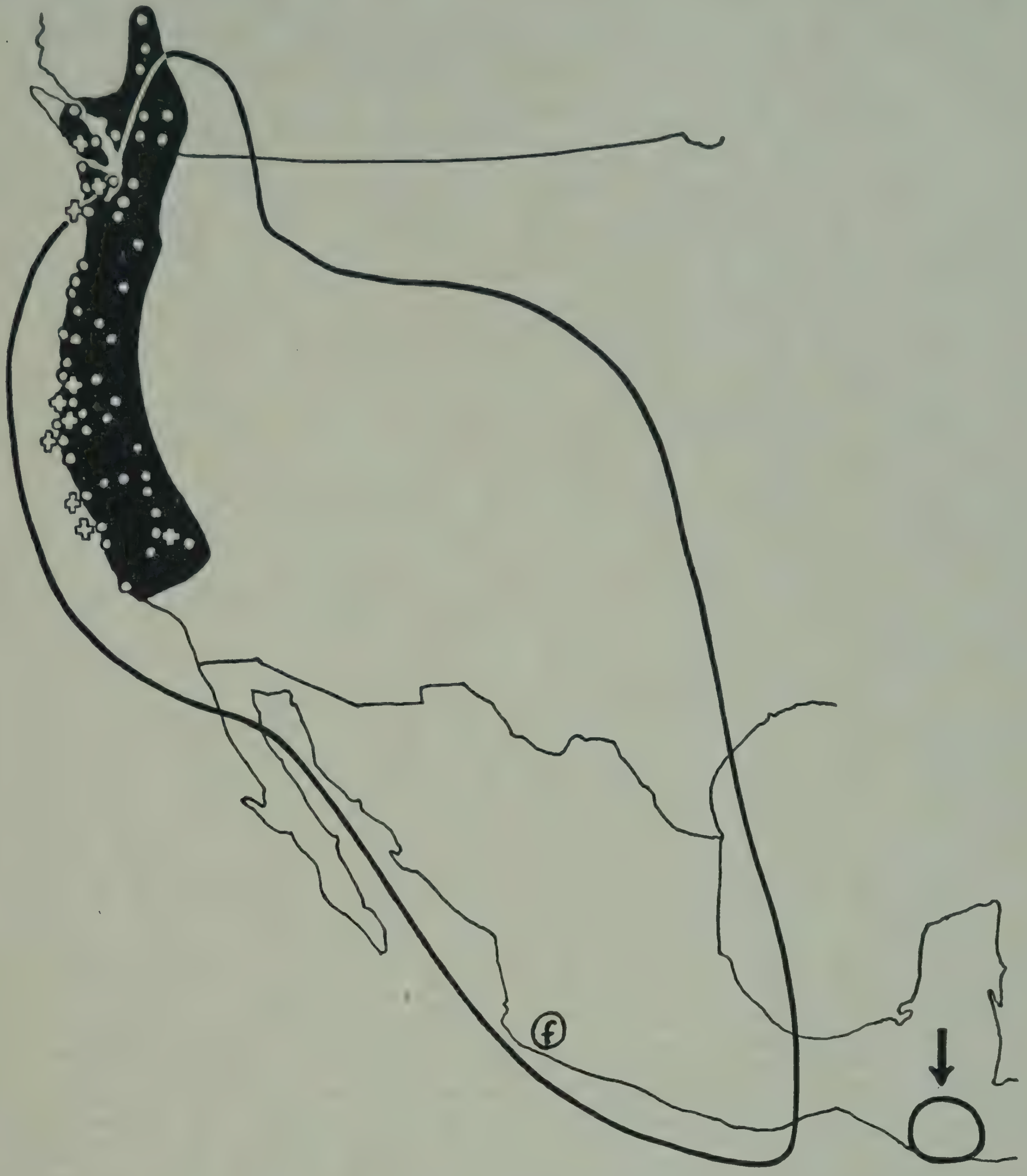

Fig. 3. Map showing the distribution of the *Drosophila pseudoobscura* group of siblings in western North America. Explanation in text. (After Dobzhansky and Epling, 1944.)

The relative abundance of *pseudoobscura* increases generally moving away from the Pacific Coast and the higher altitudes in California. Furthermore, the reproductive isolation of *miranda* is stronger against *persimilis* than it is against *pseudoobscura*, indicating that *mirabilis* and *persimilis* may have been in contact for a longer time. I interpret this situation as showing a present center of evolution for the group in the Texas-northern Mexico area, with *pseudoobscura* the dominant and most recently evolved of this particular set of species-waves.

Where two newly differentiated species are so similar ecologically that they cannot economically occur sympatrically, they may show geographical displacement similar to that of the butterfly genus *Euptoieta*. There are two principal types of these fritillaries, and each type represents a distinct species or superspecies; the two have largely complementary ranges in the Americas. *E. claudia* ranges through northern Argentina, Bolivia, the Andes, higher elevations in Jamaica and Central America, and North America. *E. hegesia* is a more tropical species, occurring at lower altitudes and latitudes, and meeting the range of *claudia* at many points. Both species feed on the same families of foodplants (W. T. M. Forbes, personal communication; E. Munroe, unpublished thesis).

In Europe, certain species of bumble-bees are known to show similar "fringing distributions" around closely related species (Richards, 1935), and Wilson and I (unpublished) have found species or superspecies of ants in several genera of Melanesia which ring

New Guinea and neighboring large island groups, on which occur closely related superspecies or species of a more variable, and at the same time a more advanced, type. I think there must be many such cases in all groups of animals. Some are already known in marine animals, if some interpretations of so-called bipolar distributions are correct (Ekman, 1953).

The most significant parts of the hypothesis are the emphasis on the center as the principal source of evolutionary change of the sort that leads to potent (generally-adapted) new species, and through them to the higher categories; and the role of density-reactive population fluctuations, expansions and contractions of range in spreading new characters and in making and breaking the contacts between populations. The idea of central change and peripheral thrust is not new. Various elements of these ideas occur in the writings of people like Darwin, Timofeef-Ressovsky, Matthew, Willis, Vavilov, Dobzhansky and P. J. Darlington, among others. However, I think that the synthesis here presented may represent the first consideration of all of the points covered as one unified concept.

The model I have discussed is a complex one— much more complex than the mentioned alternatives of division and colonization. But it is difficult to see how division and colonization can have played more than a relatively minor part as processes contributing to the evolutionary mainstream. Many of the cases that are thought to illustrate division, such as the so-called glacial relict distributions, may in fact really be stages of a unidirectional species differentiation more in line with the type I have been discussing. At least, we should be willing to consider alternative explanations of the origin of some of these patterns, no matter how popular current interpretations may be.

The colonization type of isolation and speciation is stressed by Mayr in a recent paper (1954). Mayr feels that formation of new species and major categories commonly occurs by the breaking-off of populations around the edge of a range. He singles out changes in the selective values of genes against the altered genetic backgrounds of the colonist propagules, and thinks that colonization therefore favors rapid and radical changes on this basis. But it seems that he fails to consider adequately the precise nature of the biotic differences between the original and new-colonial ranges. Particularly important here are the differences in faunas in the different ranges, especially the competitors (and also the predators). This importance is implicit in the theory of character displacement, and is well illustrated by the cases of genera radiating on oceanic archipelagoes, such as the Galapagos geospizines and the drepaniids among the birds, and *Nysius* among the (hemipterous) insects.

An equally or more important reason to discount peripheral colonists as potent new evolutionary material is found in the distribution of major groups of animals. As Darlington has shown for paussid beetles (1950) and for all the major groups of both warm- and cold-blooded vertebrates in his new book (1957), it is likely that most such groups arose in continuous or near-continuous land masses with warm, favorable climates, and then spread from these centers to smaller or less favorable areas. Darlington thinks that the large warm areas owe their evolutionary potency to their better chances of producing generally-adaptive combinations of characters that enable a species to enter various environments and prosper in most.

Darlington and I are talking about different hierarchical levels of the same process. If major-group evolution is only the extension and accumulation of normal speciation sequences, as seems now to be the general consensus, then we should not be surprised at the centrifugal patterns both processes make in their most significant operations. The only difference between them is one of scale.

REFERENCES

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. *University of Chicago Press.*

Bequaert, J. C. 1931. Color variation in the common hornet *Vespa crabro* Linnæus. *Konowia* 10: 101-109.

Brown, W. L., and E. O. Wilson. 1956. Character Displacement. *Syst. Zool.* 5: 49–64.

Chermock, R. L. 1946. Migration in *Ascia monuste phileta* (Lepidoptera, Pieridæ). *Ent. News* 57: 144-146.

Crampton, H. E. 1932. Studies on the variation, distribution and evolution of the genus *Partula*. The species inhabiting Moorea. *Carnegie Inst. Washington Publ.*, No. 410; cf. pp. 91–129.

Darlington, P. J. 1950. Paussid beetles. *Trans. Amer. Ent. Soc.* 76: 47–142.

Darlington, P. J. 1957. Zoogeography. *John Wiley*, New York.

Dobzhansky, Th., and C. Epling. 1944. Contributions to the genetics, taxonomy and ecology of *Drosophila pseudoobscura* and its relatives. *Carnegie Inst. Washington Publ.*, No. 554.

Ekman, S. 1953. Zoogeography of the sea (English ed.). *Sidgwick and Jackson Ltd.*, London.
Forbes, W. T. M. 1927. The genus *Melinæa* Hubner, with a description of a new species (Lepidoptera, Ithomiinæ). *Jour. N. Y. Ent. Soc.* 35: 23–36; cf. p. 28.
Ford, E. B. 1945. Butterflies. *Collins*, London.
Griscom, L. 1937. A monographic study of the red crossbill. *Proc. Boston Soc. Nat. Hist.* 41: 77–210.
Harville, J. P. 1955. Ecology and population dynamics of the California oak moth *Phryganidia californica* Packard (Lepidoptera: Dioptidæ). *Microentomology* (Stanford University) 20: 83–166.
Hubbell, T. H. 1954. The naming of geographically variant populations. *Syst. Zool.* 3: 113–121.
Key, K. H. L. 1950. A critique on the phase theory of locusts. *Quart. Rev. Biol.* 25: 363–407.
Lack, D. 1954. The natural regulation of animal numbers. *Oxford University Press.*
Mayr, E. 1954. Change of genetic environment and evolution. *In* Evolution as a process by J. Huxley *et al.* ed., pp. 156–180. *Allen and Unwin Ltd.*, London.
Nicholson, A. J. 1954. An outline of the dynamics of animal populations. *Australian Jour. Zool.* 2: 9–65.
Nielsen, E. T., and A. T. Nielsen. 1950. Contributions toward the knowledge of the migration of butterflies. *Amer. Mus. Novit.* No. 1471.
Richards, O. W. 1935. *Bombus muscorum* (Linnæus) and *B. smithianus* White (Hym.). *Trans. Soc. Brit. Ent.* 2: 73–85.
Vaurie, C. 1949. A revision of the bird family Dicruridæ. *Bull. Amer. Mus. Nat. Hist.* 93: 199–342.
Voous, K. 1950. On the distributional and genetical origin of the intermediate populations of the barnowl (*Tyto alba*) in Europe. Syllegomena Biologica, Festschr. *O. Kleinschmidt*, Leipzig.
Wilson, E. O. 1951. Variation and adaptation in the imported fire ant. *Evolution* 5: 68–79.
Wilson, E. O. 1953. Origin of the variation in the imported fire ant. *Evolution* 7: 262–263.

DISCUSSION

O. W. RICHARDS. Is Dr. Brown not confusing two different things: the spread of mutations within one species and the spread of an already distinct species within the range of another species.

W. L. BROWN, Jr. I am not confusing the two processes, both of which are required by the hypothesis that I have put forward. Spread of the distinct species follows its differentiation as such. The spread of mutations is a prior necessity for that differentiation.

The Significance of Ecologically Equivalent Species of Hemiptera that Coexist in Nature

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ABSTRACT

According to Gause's principle (1934), two species with similar ecology cannot live in the same region. Yet it is common knowledge that two or more closely related species of the same genus of insects occur together under apparently identical conditions. Several cases of this kind in the Hemiptera are cited, and each is analysed in terms of Nicholson's (1955) classification of requisites and the influence they have on dynamics of animal populations.

Sibling Species in the Chrysomelidae[1]

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ABSTRACT

The need for taxonomic studies of complexes of siblings, especially in the phytophagous groups, has become great. The paper describes a method of study applied to certain chrysomelid complexes, the results obtained, and the problems revealed. The principal genera discussed are Chlamisus *Raf.,* Calligrapha *Chev., and* Chrysomela *L. (=*Lina *Redt., =*Melasoma *Steph.). The method consists essentially of comparing breeding populations in the field and laboratory at selected localities, and of relating them to one another and to insects collected elsewhere on the basis of food-plants, distributions, and such feeble morphological characters as they possess. The results are taxonomic arrangements that cannot be obtained by ordinary methods of study. The principal problem is the relating of slightly different allopatric forms, which are difficult to compare adequately.*

The term sibling species was proposed by Dr. Ernst Mayr in 1942 simply as a convenient term to designate those species that are morphologically very similar or indistinguishable. Sibling species possess specific biological characteristics and are reproductively isolated like other species of bisexual animals. Thus they are similar to other species, except that they are more difficult to separate, and the species considered siblings by one generation of entomologists are sometimes considered well-characterized by the next generation.

Because they are difficult to distinguish, sibling species have been recognized as a special problem for almost a century by entomologists, who have called them also phytophagic species, physiological races, physiological species, and cryptic species. The need for taxonomic study of complexes of siblings has become increasingly great in both the purely scientific and in the economic fields. To mention only two examples of such need, the problem in the Culicidæ has long been recognized, and it is almost certain that the spruce budworm, so-called, which is perhaps the most important forest insect in North America, is not a species but is, rather, a complex of siblings. However, our knowledge of sibling species of insects lags, partly because studies on them are difficult and time consuming, and partly because of the inadequate concepts and methods that have been applied to their study.

For our purposes, we shall define sibling species as very similar species that have been segregated primarily or in part by differences in the ecological relationships of the beetles concerned. So defined, sibling chrysomelids have been studied by six North American authors, who have considered species of seven genera belonging to six subfamilies.

The earliest of these studies was published in 1864 by Benjamin Walsh. Walsh defined two categories, the phytophagic variety and the phytophagic species. Phytophagic varieties were forms distinguished by slight morphological differences that were correlated with differences in food-plants, when it was believed that the forms interbred. Phytophagic species were similar to phytophagic varieties, except that they did not interbreed. Thus Walsh's phytophagic species are sibling species in the sense of Mayr. Walsh was far ahead of his time. He made reproductive isolation his criterion of the species, and he recognized sibling species as such in a day when degree of morphological differentiation was usually the arbitrary criterion. Walsh wrote largely of other insects, but he did consider the chrysomelid genus *Calligrapha*, which is discussed below.

The next author to consider sibling chrysomelids was Frederick Knab who, in 1909, noted that the determination of food-plants of the different species of *Calligrapha* is the key to the proper understanding of them. On the basis of food-plants and rather feeble morphological characters, Knab segregated two species from the complex of siblings that was known as *Calligrapha scalaris* (Lec.).

William Colcord Woods was the first to test the ability of larvæ from certain populations to live on the different food-plants of other populations. On the basis of such tests, and on differences in colour of adults and in setal patterns of larvæ, he segregated in 1918 three species of *Altica* Fab. from the complex that had been known as *Altica ignita* Ill. After similar studies on *Galerucella* Cr., he segregated in 1924 three species that had been confused together as one species and five that had been confused as another.

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In 1926 Norman Criddle segregated two species of *Physonota* Boh. by noting differences in food-plant, which he correlated with slight morphological differences.

The most recent paper on sibling chrysomelids is that on *Paria* Lec., which was published by John A. Wilcox in 1954. Two species of *Paria*, one with eleven named colour varieties, had been recognized in the United States and Canada. Wilcox has segregated nine species, and his studies are incomplete.

My own studies of sibling chrysomelids have been concerned largely with species of *Chlamisus*, *Calligrapha*, and *Chrysomela*. The genus *Chrysomela*, incidentally, is not the *Chrysomela* of most authors; it is the genus that has been known in America as *Lina* and in Europe as *Melasoma*. My studies are incomplete, as such studies always are, but they have resulted in each genus in an arrangement of species that could not possibly result from a study of museum collections. In the many, many comparable genera in the Insecta, arrangements based on museum specimens must be considered provisional until they have been checked by studies made in the field and laboratory.

The genus *Chlamisus* Raf. (=*Chlamys* Knoch) is represented in the United States and Canada by a rather large number of species, most of which have been confused under the name *gibbosa* Fab. The adult beetles are peculiar little things. They range from three to five millimeters in length and are almost cubical in form. They are metallic and very roughly sculptured. Their larvæ are case-bearers. The species feed on a variety of plants, mostly shrubs and trees, and the food-plant is usually the best identification character that a species possesses (Brown, 1943). In easternmost Ontario, there are five species. One feeds only on the low blueberry, *Vaccinium angustifolium* Ait., and one only on the alder, *Alnus rugosa* (Du Roi) Spreng. One feeds on the leatherleaf, *Chamædaphne* Moench, and one restricts itself to the subgenus *Eubatus* Focke of the genus *Rubus* L. The fifth restricts itself to a single species of willow, *Salix bebbiana* Sarg. In New Brunswick, one species occurs on the sweetfern, *Comptonia* L'Her., and one on strawberry, *Fragaria* L. Two species occur on hazel, *Corylus americana* Walt., in southernmost Ontario. One breeds on *Rubus* in southeastern United States, and one on sycamore, *Platanus occidentalis* L., in central and eastern United States. Thus the species are highly restrictive in their feeding. Most of the species of the complex are completely unstudied. One cannot segregate the species mentioned above if he works only with the material that accumulates in collections, or, except in a few cases, if he works with descriptions alone. But if one compares series from different food-plants, he can separate them by differences, usually slight, in colour and sculpture, or by differences in the form of body parts. However, there are two complications, both centering on the willow-feeder. The first concerns the male genitalia of that species.

Of the species that I have mentioned, two lack males, and the males of two others are scarce. But only one of the species has male genitalia that are characteristic. The males of all but three have the median lobe of the genital organ like that figured in the left-hand drawing of Fig. 1. The median lobe is a flattened tube. When it is mounted in balsam on a slide, it is transparent enough to show the armature of the internal sac, which is shown in the figure. In beetles from colonies on the willow, *Salix bebbiana*, about thirty per cent have the organ like that figured on the right. The remainder have the organ like that figured on the left. The commoner type of organ differs from the other in having the apex pointed and distant from the median orifice, in having the paired organ of the internal sac much more elongate, and in having the basal truncation of that organ, which is oblique, much shorter. Ordinarily one would suspect two species strongly characterized by the four differences in the male organ. But the beetles are inseparable by other characters; they restrict their feeding to one and the same species of willow; and the scarcer form has been found only in the company of the commoner form. Dimorphism was suspected, and it was demonstrated by rearing (Brown, 1944). The progeny of seven females were reared, and two of them produced males with genital organs of both types.

The second complication concerns the relating of allopatric forms that are identical morphologically but that depend on different food-plants (Brown, 1952). The willow-feeder, except for the males with genitalia of the uncommon type, cannot be distinguished

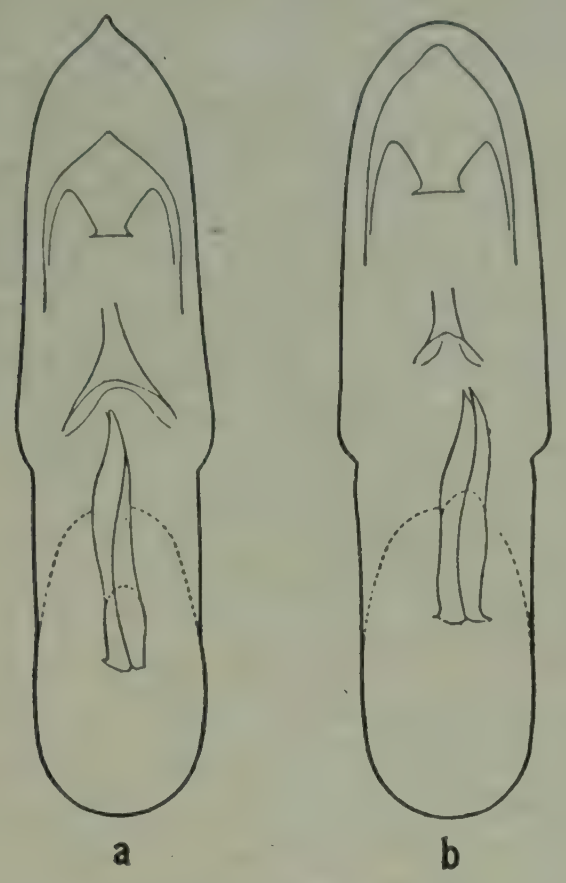

Fig. 1. Median lobes of genital organs of *Chlamisus bebbianæ* (Brown). a, commoner form. b, scarcer form. (After Brown, 1944).

from one of the hazel-feeders of southernmost Ontario. It seems most unlikely that a species restricting itself to one kind of willow in eastern Ontario would restrict itself to hazel in another faunal region. Both of these forms cannot be distinguished from a form that is common on alder in Nova Scotia, a form that is quite different from the alder-feeder of Ontario. I suspect three sibling species on the three food-plants, but this has not been demonstrated.

The problem in the genus *Calligrapha* Chev. concerns the species that have been confused together under the name *scalaris* (Lec.). In 1864 Walsh noted that specimens of *scalaris*, so-called, from the wild plum, *Prunus americana* Marsh., and from dogwood, *Cornus* L., were smaller than specimens from elm, *Ulmus* L., and basswood, *Tilia americana* L. He suspected that the differences were due directly to the food, so he referred all of the forms to *scalaris*. Knab (1909) restricted the name *scalaris* to beetles occurring on elm and basswood, but the species actually are more numerous and restrict their feeding more than Knab suspected. Eleven species of the *scalaris* complex are known from Ontario. Knab described two of these, one from dogwood, the other from hazel, and Schaeffer described a third, which feeds on alder. My studies (1945) have concerned the remaining eight, of which five, one species to each row, are shown in Fig. 2. The species all show the same colour pattern, which varies considerably in each. In fact, the spots on the two elytra of one specimen are never exactly the same. It is usually difficult or even impossible to identify specimens when the food-plants are unknown, because most of the species lack characters except for more or less inconstant characters in the colour pattern. The species figured in the top row feeds on the birch, *Betula papyrifera* Marsh. It can be distinguished from the others only because its elytral epipleuræ are dark and metallic, rather than pale. The species figured in the bottom row feeds on hornbean, *Ostrya virginiana* (Mill. K. Koch). It tends to be more heavily maculate than the others and differs from all others in having the elytral epipleuræ yellow in sexually mature individuals. The species of the second row is a northern basswood-feeder, and that of the fourth row is a southern basswood-feeder. The former lacks males and is relatively easy to identify because the colour pattern varies little, and some of the markings are fairly characteristic in form. Males of the southern species are as numerous as females, but individuals are almost impossible to identify, except when associated with food, because of great variation, many specimens resembling average specimens of other species. The species of the third row is an elm-feeder. It is quite variable, and, like the hornbean-feeder figured in the bottom row, it has few males. Like the adults of this group, the larvæ are sometimes inseparable, sometimes separable by slight differences in colour, but then usually only in series because of variation and overlap.

Three of these species occur in eastern Ontario. They are the basswood-feeder figured in row two, the elm-feeder, row three, and the hornbean-feeder, the bottom row.

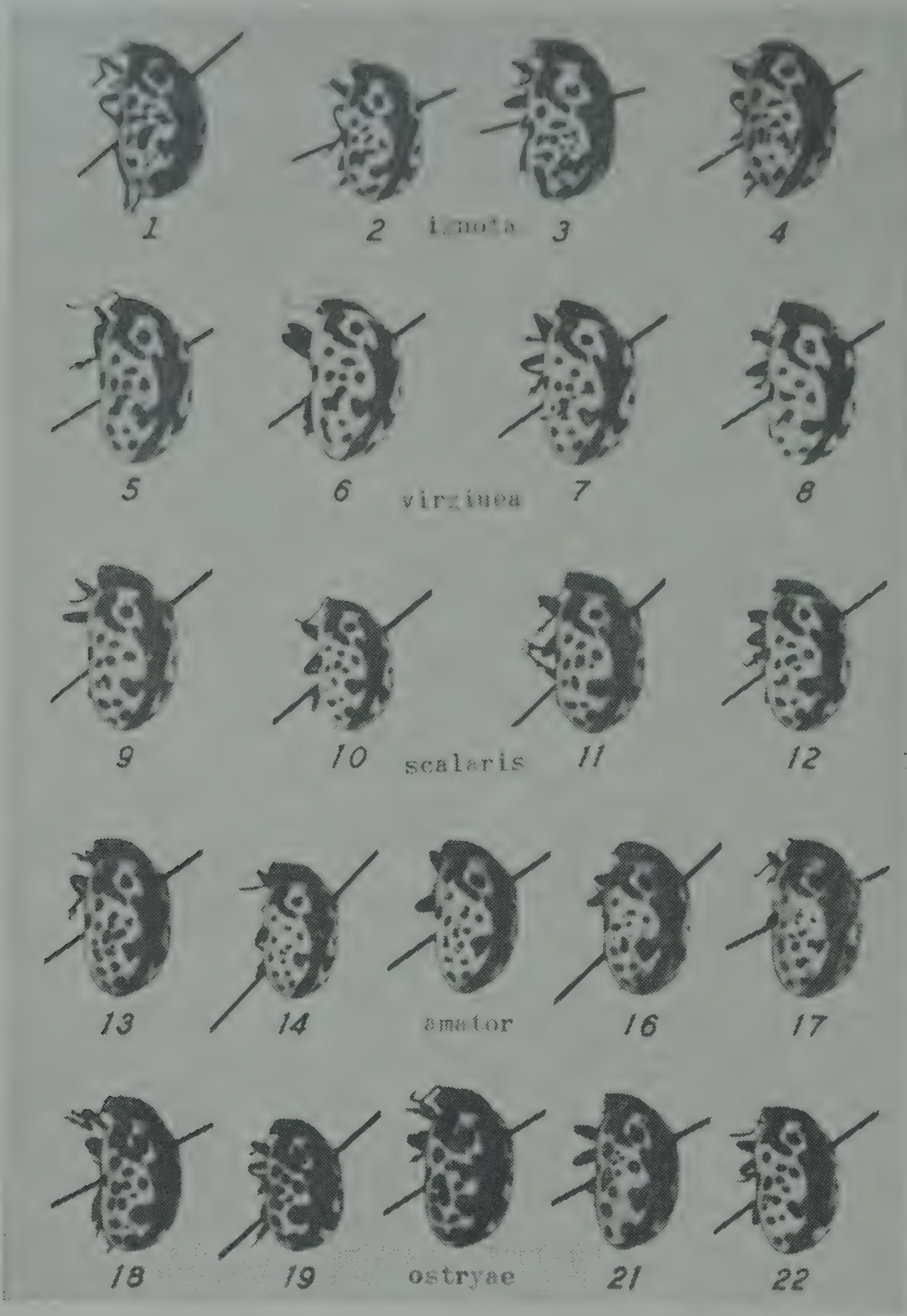

Fig. 2. Species of *Calligrapha* Chev. (Modified after Brown, 1945).

Adults of these were confined in the laboratory for eggs, and larvæ of all were reared with little or no mortality on the parental food-plants. Then newly hatched larvæ of each were confined on the food-plants of the other two species. Larvæ of the elm-feeder, given basswood, produced some stunted adults after suffering heavy mortality. In all other cases, all larvæ died without attempting to feed on the plants supplied to them, although some larvæ of the basswood-feeder were able to moult once because they fed upon their weaker fellows.

The third genus, *Chrysomela* L., is a holarctic genus with two natural groups that include siblings (Brown, 1956). Fig. 3 shows the colour patterns of the North American species of these groups. Numbers seven to 29 of this figure represent eight forms that were confused together under the name *interrupta* (Fab.) or with the European species *lapponica* L. Incidentally, *lapponica* of European authors is certainly a complex of siblings. The American species present a difficult problem because their adults differ only by very inconstant characters in colour and size, and the larvæ are virtually without specific characters. However, the forms tend to replace one another geographically, and when two or more species occur in one locality, they live on different food-plants. Numbers 7 to 9 represent an alder-feeder that is restricted to southeastern United States. Its range adjoins or perhaps overlaps slightly that of a willow-feeder represented by numbers 20 to 22. Adults of these species can usually, but not invariably, be distinguished by differences in the elytral spots. The willow-feeder cannot be reared on alder. It occurs throughout most of the United States east of the Rocky Mountains. In the east it reaches its northern limit

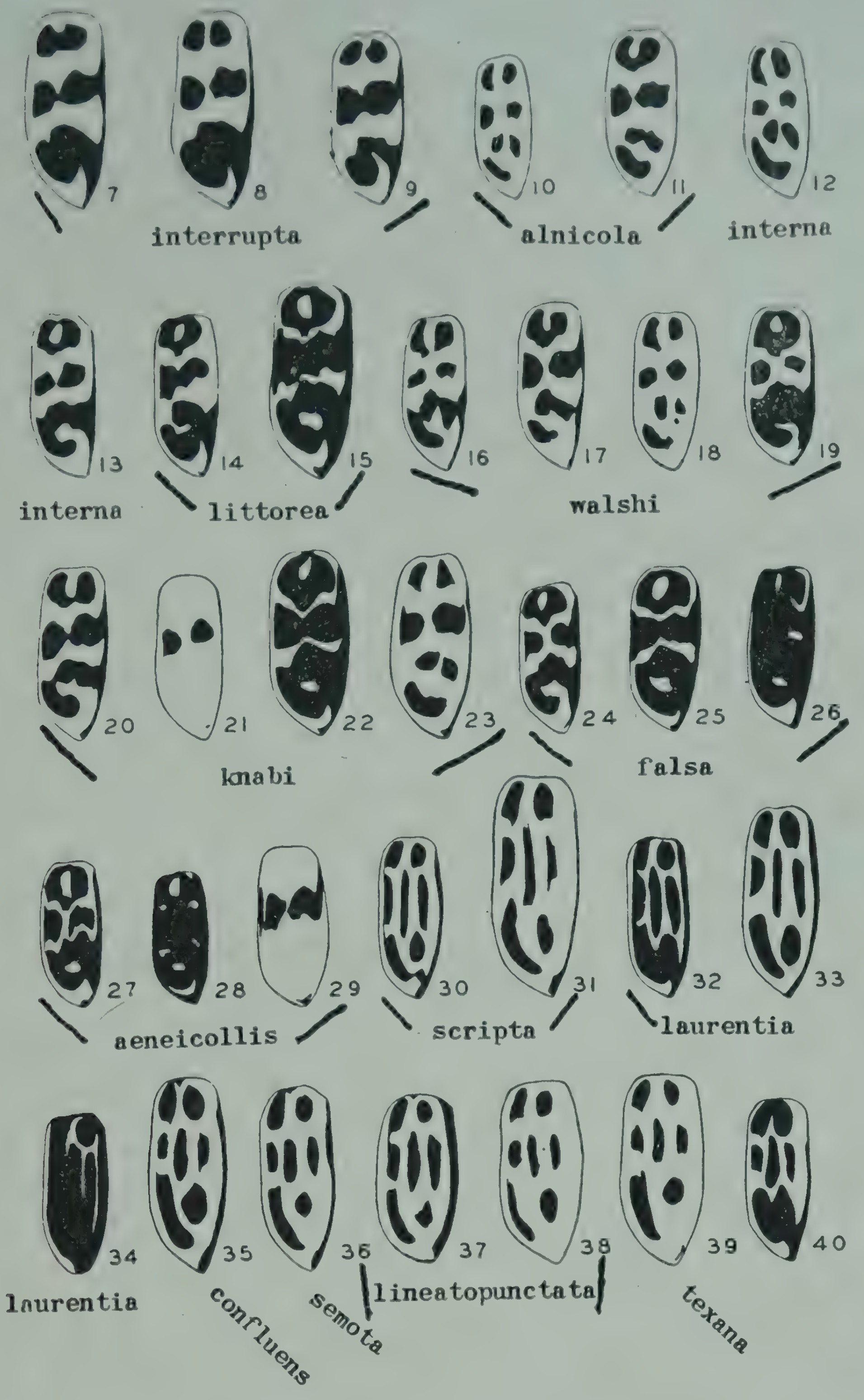

Fig. 3. Left elytra of species of *Chrysomela* L. (Modified after Brown, 1956).

in the Lake Erie region, where it occurs with two other species, a balsam poplar-feeder, numbers 16 to 19, and a second alder-feeder, number 10. Both of these species find their southern limits in that region. This alder-feeder is smaller and much paler than the willow-feeder and will not be confused with it. But the poplar-feeder is intermediate and quite variable in size and colour. The darkest specimens of the poplar-feeder cannot be distinguished from average specimens of the willow-feeder, and the most pale are like specimens of the alder-feeder. Neither the poplar-feeder (with rare exceptions) nor the alder-feeder can be reared on the food-plant of the other. Both the poplar-feeder and the willow-feeder can be reared on the food-plant of the other, but neither breeds on the food-plant of the other in nature. The alder-feeder occurs, with moderate geographic variation, from New York and Newfoundland to Alberta and Great Slave Lake. West of the Rocky Mountains, it is replaced on alder by a form that averages larger and darker, numbers 12 and 13, which in turn is replaced west of the coast range by a form that averages still larger and darker, number 14 and 15. Perhaps these three alder-feeders should be considered subspecies of one species. They are separated by mountain barriers, and there is no evidence of clines. All vary geographically, the two western ones becoming progressively darker to the north. In any case, I consider them distinct taxonomically, for their differences are of the same order as those that distinguish species in the group. From Newfoundland and Labrador to northern British Columbia and Alaska, there occurs a species, numbers 24 to 26, that feeds on both poplar and willow. Some specimens of it cannot be distinguished from some of the two western alder-feeders, numbers 12 to 15, with one of which it occurs, or from specimens of the poplar-feeder, numbers 16 to 19, or from specimens of the southern willow-feeder, numbers 20 to 23. The last species of the group, numbers 27 and 28, is a small, dark willow-feeder that occurs from central British Columbia to Colorado and California. Now in this group, if one ignored the locality and food-plant labels, he could identify with confidence only a small percentage of the specimens in our collection. But if he ignored the specimens, he could sort the pins without error by reference to the labels alone.

I have noted geographic variation in the group. Most of the forms vary geographically and clinal variation within a species may produce forms differing as much as relatively well-characterized species. Thus, in the willow-feeder of the United States, the spots are fused in part in eastern specimens, numbers 20 and 22, but are nearly always completely disjunct, number 23, in western specimens. The cline that joins these forms is readily demonstrated.

There is also dichromatism in the group, and this occurs in eggs, larvæ, and adults. In most of the forms, larvæ of the last instar may be either dark or pale, and adults occur in which only two spots have developed on each elytron, numbers 21 and 29. The frequency of the dimorphs often varies geographically.

I suspect a very limited amount of introgressive hybridization between some sympatric species of this group. The northeastern alder-feeder is sympatric with the poplar-feeder and with the species that feeds on both willow and poplar, and it has been hybridized with both in the laboratory. The hybrids are quite viable. Moreover, species discrimination appears to be weak in the genus. Rarely one finds distantly related species cross-mating in nature. I once found in a mixed colony four individuals of the willow-feeder, numbers 20 to 23, copulating with individuals of the distantly related *C. scripta* Fab., numbers 30 and 31. Mating in this mixed colony may have been at random. The siblings that have been tested in the laboratory show no species discrimination. However, adults behave abnormally in confinement and copulate much more freely than in nature. In eastern Ontario, the northeastern alder-feeder and the poplar-feeder differ only in that the adults from poplar are darker on the average. The eggs and adults are not dichromatic in either species there. In the single colony of the poplar-feeder known in southernmost Ontario, the adults average darker still, although the range of variation is the same, and they are dichromatic; also the eggs are sometimes deep yellow, rather than whitish. Now yellow eggs and dark and dichromatic adults are characters of the willow-feeder that is abundant in that region. The willow-feeder is not known to breed on poplar, but it often feeds freely on poplar in early spring. And it is known to cross-mate rarely with a species to which it is not closely allied. So it is possible that the willow-feeder has invaded the colony of the poplar-feeder and that some introgressive hybridization has resulted.

Numbers 30 to 39 of Fig. 3 represent a group of species that have been confused together, but they are less difficult than the others. Numbers 32 to 34 represent a northern willow-feeder that differs from a southern poplar and willow-feeder, numbers 30 and 31, only in averaging smaller and darker. Such colour differences in this genus are frequently due to clinal variation. However, in this case, as in some other cases in the genus, field work has shown that the two forms are strictly allopatric, although no physical barriers separate them, and preferred food-plants of both are abundant in the intervening area in which neither species occurs. Their isolation is complete and is strictly ecological. I consider such allopatric forms good species. This seems justified on historical and ecological grounds, regardless of the genetic potential, which is unknown in all such cases in the genus.

In the genera that I have discussed, the beetles live in colonies. The larvæ feed on leaves and are easily reared. Thus they lend themselves to study. The species that live on one food-plant in one locality are not or are scarcely sibling to one another. With few exceptions, as perhaps in *Chlamisus*, the siblings differ morphologically in some stage or to some degree. The differences are often inconstant and may be obscured by variation, both individual and geographic. There seems to be only one satisfactory method of segregating such species. This consists of comparing breeding populations in the field and laboratory at selected localities. The populations can then be related to one another, and to insects collected elsewhere, on the basis of behaviour, distributions, and their feeble morphological characters. The greatest problem is that of properly relating slightly different allopatric forms, which may require much knowledge of distributional patterns and of geographic variation, as in *Chrysomela*.

REFERENCES

Brown, W. J. 1943. The Canadian species of *Exema* and *Arthrochlamys*. *Canadian Ent.* 75: 119–131.

Brown, W. J. 1944. The dimorphism in the male copulatory organ of *Arthrochlamys bebbianæ* Brown. *Canadian Ent.* 76: 70–72.

Brown, W. J. 1945. Food-plants and distribution of the species of *Calligrapha* in Canada, with descriptions of new species. *Canadian Ent.* 77: 117–133.

Brown, W. J. 1952. Some species of *Phytophaga*. *Canadian Ent.* 84: 335–342.

Brown, W. J. 1956. The New World species of *Chrysomela* L. *Canadian Ent.* 88, suppl. 3: 54 pp.

Criddle, N. 1926. A note on the synonymy of certain species of *Physonota*. *Canadian Ent.* 58: 207–208.

Knab, F. 1909. Some species of *Calligrapha*. *Proc. Ent. Soc. Washington* 11: 83–87.

Mayr, E. 1942. Systematics and the origin of species. *Columbia University Press*, New York.

Walsh, B. D. 1864. On phytophagic varieties and phytophagic species. *Proc. Ent. Soc. Philadelphia* 3: 403–430.

Wilcox, J. A. 1954. Leaf beetles of Ohio. *Ohio Biol. Survey Bull.* 43, vol. 8(3): 353–506.

Woods, W. C. 1918. The biology of Maine species of *Altica*. *Maine Agr. Expt. Sta. Bull.* 273: 149–204.

Woods, W. C., and H. C. Fall. 1924. The blueberry leaf-beetle and some of its relatives. *Maine Agr. Expt. Sta. Bull.* 319: 81–140.

DISCUSSION

C. D. MICHENER. Are there large unoccupied niches, for example, areas where the food-plant willow is not attacked by any species, or do species of other genera then occupy the niches unoccupied by the genera you have discussed?

W. J. BROWN. This is a difficult question. There do exist large areas where willow is not attacked by any species of *Chrysomela*. Whether species of other genera completely occupy the niche is not known.

F. I. VAN EMDEN. Similar problems are found, of course, in parasitic species and in other ecological groups. The terms used for them (sibling species, biological races, etc.) do not matter, the important fact being that they are less strongly differentiated from one another than are the forms normally termed species. In the future, there will be discovered new and more subtle characters in the cases where actual species have evolved.

W. J. BROWN. The important point is that these very similar forms live in nature as species, i.e., that they do not normally interbreed.

R. L. USINGER. What are the host preferences of hybrid beetles?

W. J. BROWN. The hybrids will feed on either of the parental hosts.

M. H. HATCH. Apparently some of these species are parthenogenetic. If so, does not a different principle of speciation hold for them?

W. J. BROWN. Obligatory parthenogenesis certainly occurs in *Chlamisus*, *Calligrapha*, and in some other genera of the Chrysomelidæ. But speciation apparently preceded the parthenogenesis; for purposes of convenience in taxonomy, the species can be treated as if that were the case. Of course, the evolution of the parthenogenetic forms is governed by principles different from those concerned in bisexual forms.

On the Recognition of the Species

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ABSTRACT

The difficulties of the problem and the nature of the species are discussed. Definitions and tests are shown to refer to stages in the life of the species, which is a continually developing entity. The establishment of specific nature is shown to precede the regular development of morphological character and genetic discontinuity. The species at its birth is not visibly recognizable; a possible test for its detection is suggested. The early stages of specific development are mostly distinguishable by one or other of the four normal lines of approach: geographical distribution, morphology, embryology, and genetics. In distribution the great importance of proximity of races, as distinct from overlap, is stressed; colonies of one and the same race, or two distinct species, can exist in proximity; but not of two conspecific races. "Intermediates" and the use and abuse of structural character are discussed, as are the value of structural characters in the egg and larva, and the results of both inter- and intraspecific cross-breeding and the possible help to be derived from the chromosomes. Failure to distinguish preracial variability for what it is, is shown to be a source of error, as is the faulty use of the term "subspecies". The paper ends with a suggestion that the Congress should adopt some official definition of that term on lines that have been suggested by several systematists during the past fifteen years, which have actually been followed by the author in his own work for over thirty years.

Whatever line of entomological science is followed, the lasting value of any work will depend, ultimately, on the accuracy of its systematic foundation; and that to a great extent rests on the recognition of the species. Speciation is of no great complexity up to a certain point: that of the problem presented by races of superficial similarity, yet possessing some attributes that might indicate speciation. Are they species, or races of one species? It is generally accepted that superficial features though serving to identify established species are no criterion of speciation. All the same it is obvious from contemporary literature that many writers practically accept a general, superficial similarity in two insects as an indication that they are races of one species and class them as such on almost any pretext. But it is less generally appreciated that many morphological characters (so-called), are of the same nature as the superficial; they serve to identify but are no criterion of speciation, because they are not constant to a given species. Isolation is another criterion often put forward as a proof of specific unity; but unless the two races are very widely separated indeed, this is mere assumption liable to be disproved at any time which has often happened. Many attempts have been made to define a "species"; but they fail when most needed and leave the systematist guessing. Why? For very obvious reasons. The species is a continually developing entity; and definitions fail because such an entity cannot be defined in finite terms. All definitions but define given stages in the species' life. A definition that would cover every stage of its existence would only be a statement that a species is an entity developing continuously on divergent lines from other existing entities. The systematist familiar with many categories of specific development easily appreciates this. All evolution has been and is but a drawing away from an existing present; and while many stages are sharply marked, others are not; many are apparently an advance, many merely indifferent, change possibly necessitated by other change. The development of the androconial scale in the genus *Erebia* illustrates this indifferent change very clearly. Out of some 76 known species, 27 have these scales. It has been shown that they have passed through several stages of development (Warren, 1936), but there is no ground for assuming that the species with the scales are in any way better suited to their common ecology than those without them. Yet the development of the scales represents a drawing away from the earlier simpler types, which are more similar to the ordinary scale, as well as from each other, for in each case the development of the androconial scale has become correlated to speciation. Variability, the medium of evolutionary change, displays in this genus (*Erebia*) a very striking phenomenon. The extreme degrees of variability in both the superficial sphere (colour and pattern), and the morphological sphere (genitalia), never coincide. The degree of variability that is observable in these spheres increases and decreases independently (Warren, 1937b). This is not the result of chance or ecologically engendered variation but represents definite stages through which races of all species pass, for races of many species living under widely different geographical conditions are found to display corresponding degrees of variability. Finally, to a great extent variability declines, and one finds a stabilized race that differs little from the single-race species. These races are one of the problems of systematics. There are many who say that sterility between hybrids is the sole criterion by which such questions can be resolved. This requires qualification. Experiments in interspecific cross-breeding have shown that sterility between hybrids is by no means always absolute, or even that when fertility follows it is at all constant in degree. In fact this test frequently breaks down exactly in these cases where other tests also encounter difficulty. The degree of sterility or fertility between hybrids also seems to vary according to the mere individuality of the insects concerned in the experiments; different workers get different results, and on occasions it has been shown the result depends on the sex of the parents in the original cross, hybrids of reciprocal crosses displaying a different degree of fertility (Hovanitz, 1949a). In all this we have but a demonstration of what is obvious in many other ways, that the species is a continually developing entity. The man who asserts he will only accept speciation on the strength of sterility between hybrids is in fact saying that he will only accept a species as such at a given point in its existence. If the species is to be limited in this way, why start at sterility among hybrids? Why not at the more absolute stage of primary sterility when hybridization is impossible? These are obviously but two sharply marked stages in specific development. But what of those cases where fertility between hybrids exists in unpredictable degree? This is clearly another, and earlier stage, but still there is no reason to suppose it is the first. The uncertainty caused in the minds of adherents to the sterility theory has led to the suggestion that a certain degree of fertility constitutes a prespecific stage that has been called a "semispecies" (Lorkovic, 1952b and 1953). But the only criteria given for distinguishing such "semispecies" was that hybrids might be "partially" fertile, while in true species hybrids should be "wholly or almost" infertile. This is only a difference in words. But the idea led to the errection of numerous "semispecies" for other assumed reasons. Actually I was able to prove some such races to be true species by biological and other data (Warren, 1955b). Quite apart from this, a group of homogeneous subspecies (or races), constitute a species in its most obvious appearance; in what way can an entity which is said to embrace a number of such subspecies (as the "semi-species" was supposed to do) differ from a species? To introduce such undefinable categories is but to complicate, not simplify, any question. When considering these various stages of advancing sterility, it is instructive to note that a progressive advance in morphological character is also evident. Such characterization ranges from the non-constant character in the stabilized subspecies to absolute constancy of characters in the single-race species. Whatever uncertainty may exist in the early specific stages (varying fertility), no doubts of either morphological or genetical nature ever exist in the later (absolute sterility). Time resolves all questions of speciation. It is incontestable that both morphological character and genetical discontinuity, as specific attributes, are products of time. They become partially apparent in the specialized race in time and for their further development are dependent on time. To this extent such attributes follow on speciation, *which is an essential condition that must precede their regular development.* The first approximation to the specific stage is detectable in the specialized race (subspecies) of stable nature. Such races may, or may not, have become specific entities; they develop incipient morphological and genetical characteristics, the former inconstant, the latter inconclusive. The single-race species of restricted distribution is obviously little removed from such a race. Yet some change has taken place; it is capable of development on independent lines, and its characteristics will become more and more accentuated with the passage of time. It is unquestionable that it is during the prespecific racial stage, when stability is preserved by isolation, that the most fundamental of all specific attributes originates. The race becomes a physiological unity, *a condition causing an obliterating indifference to all living creatures other than its own, now unique, kind.* This condition can only have grown in time; the many differing degrees of racial development testify to this. But once established, the race has become a species capable of developing its latent components to the utmost but debarred from adopting others; this is specific isolation. Cross-breeding experiments have shown one undeniable fact of great importance. All closely related species can be crossed in captivity. This applies to all congeneric species and many that are not. Yet in nature the hybrid is an extreme rarity; except in a few cases that will be referred to later, it scarcely ever appears. How many collectors have found a natural hybrid in a lifetime? In fifty years collecting I never have. Among my friends three have taken hybrids between *Lysandra coridon* and *Lysandra bellargus*. But many of the supposed hybrids among the Lycænidæ are probably only colour aberrations; this has been proved in one case (Pierce, 1925). I have obtained data and specimens of *Erebia* from collectors and museums from all over the northern hemisphere but only twice have heard of a natural hybrid, each time a cross between *Erebia epiphron* and *Erebia flavofasciata*, and strangely enough both from the same locality with an interval of twenty-five years. I was able to examine specimens of this hybrid in detail and establish its identity beyond question (Warren, 1937a). Why is this hybridization to which there is no physical barrier so rare an occurrence? There is every occasion for such pairing between related species in countless districts where they swarm in a common environment, but they do not cross. In this, one sees the power of physiological specific unity, obviously of as much or more importance to the development of the species than geographical isolation, which is more liable to be broken through. It is this physiological force alone that prevents the appearance of countless hybrids everywhere. When on rare occasions hybrids do appear, this most probably is accidental, or the result of a state of pathological deficiency, but more probably the former. Should anyone doubt this, let him watch a male butterfly jostling among a number of insects in search of a possible mate. He is as indifferent to the other species of butterfly as to some beetle that crosses his way. Or again, watch the males of *Lasiocampa quercus* flying about a rock where a newly emerged female is resting. How often has anyone seen a male of another species join the throng? Such is the normal way of insect life everywhere. A break from this can only be accidental or result on pathological deficiency. In some wholly abnormal cases in the genera *Colias*, *Pyrgus*, and *Anthrocera*, certain species hybridize fairly freely when they meet. Long ago Zeller noted this frequent mating between some species of *Anthrocera* in "a condition of perfect liberty". Yet these species remain distinct, probably because subsequent mating between the resulting hybrids and the parent species would be improbable, for in nature abnormal individuals will rarely succeed in mating. Nature abhors the abnormal as much as the vacuum, a natural phenomenon that probably has a greater restraining influence on abnormal varietal strains than the genetical laws of heredity. As already suggested it is most probable that these irregular pairings are accidental. All these cases, though relating both to butterflies and moths, have a marked characteristic in common. The species concerned are extremely similar. In *Pyrgus* and *Anthrocera* this similarity is so great that identification is sometimes impossible without dissection. The frequency of crossbreeding between such species may indicate nothing more than mistakes by the insects themselves. The males of some *Anthrocera* species display a tendency to "assemble", which suggests that similarity in this genus is not always restricted to appearance. If such cross-pairing is not the result of mistakes in identity by the insects, why is it that this frequency of hybridization is unknown between any of the more distinctly marked species of *Anthrocera*, *Pyrgus*, or *Colias*? Hovanitz noted (1949a), of cross-pairing between *Colias eurytheme* and *Colias philodice* in nature, that mating took place soon after emergence and appeared to be at random. In other words the males of the two species to a great extent fail to recognize their own kind, and the females must also be deceived. But these accidental pairings are a natural demonstration of what would be the universal order, were it not for the controlling power of physiological, specific unity. The number of hybrids that may result on any irregular cross appears to be entirely a matter of chance, some incompatibility of nature intervening and disorganising the normal order of fertilization. But such inhibition of fertility would not be sufficient of itself to keep the species pure were it not for the fundamental, physiological barrier to cross-pairing that reduces such accidental unions to a degree of insignificance and for the secondary barrier to the mating of hybrids. In attributing irregular pairings to accident, one implies that insects are guided by intelligence; some may hold this to be impossible, but if instinct alone were responsible these mistakes would not occur. There are other actions that demonstrate insects possess a power of recognition of objects, which is not instinct for again mistakes are frequent. For example the efforts of individuals of *Macroglossum stellatarum* to suck nectar from artificial flowers that have no scent is proof that sight has been the incentive that led the insect to assume it would find what it wanted. Again, the fact that many satyrid species resting in a tree will follow downward a stone thrown up to them is another demonstration of the same intelligent use of sight.

By what means then can the species be recognized in the early stages? The first period of fixity of the race as a unique entity will never be observable. The only possible test would be the liberation of specimens of one race among those of another *in their natural habitat*. Their reactions would give an indication of the extent to which their individuality had become a unique quality. The earliest stages in which the effects of specific isolation have become reflected in visible attributes should be recognizable by one or a combination of the four usual lines of approach: geographical distribution (including ecology); morphology; embryology, and genetics; the first two being the most practical and definite. We will consider them in this order.

GEOGRAPHICAL DISTRIBUTION

In borderline cases the first question likely to be asked is whether the two insects occur together or not. Zones of contact are often mentioned, and differentiation between such zones and cases of overlap much emphasized. My own observations led me long ago to the conclusion that such differentiation is purely theoretical. The presence of even a single specimen of a distinct race among members of another race is proof of overlap. I have recorded a number of such cases in *Erebia* species (Warren, 1955b). It often happens, however, that the second race is found to be located in proximity though not apparently in actual contact. The fact that we know a single specimen can pass between two races at times proves that close proximity is of as much significance as actual, observable overlap; mingling of the two races can occur. This can always be accepted where close proximity of two races is known, even if no specimens are actually found that have passed from one race to the other. Barriers that separate such localities are probably never insurmountable. The incompleteness of barriers between races has attracted attention outside the ranks of entomologists also. It has been pointed out that even apparently absolute barriers are often not wholly so (Mayr, 1949). A good example of proximity is provided by the range of *Erebia melampus* and *Erebia sudetica* on the east and west sides of the Great Scheidegg in the Bernese Alps. The species are abundant on opposite sides of the watershed, and *E. sudetica* actually attains the summit in one place. Between this and the nearest colonies of *E. melampus* stretch one or two miles of open alps. This area is almost devoid of Lepidoptera, owing to the presence of large herds of cattle that graze the ground. Strong-flying species pass across this area and occasional specimens of either *E. melampus* or *E. sudetica* may do so too. No ecological barrier exists, and the altitude is normal to both species. A much more serious barrier in the case of such mountain species is a deep valley. The normal flight habit of high alpine species checks their rising any considerable height into the air, so if they fly out to cross such a valley when they find themselves high above the ground as the sides of the valley drop away they drop to earth, and on descending a little way will soon remount to their normal altitude. But even in such conditions accidental transport cannot be ruled out. I have taken *Erebia pluto*, normally located between 7,000 and 9,000 feet, just over 4,000 feet. Such accidents can in certain circumstances become a recurring phenomenon. At Martigny in Switzerland where the Drance from the Great St. Bernard Pass joins the Rhone, the level of the valley is about 1,500 feet. It is very hot and much affected by strong winds from the mountains. Many alpine species get drawn down to the valley here: *Parnassius mnemosyne*, normal altitude 3,000 to 5,000 feet (Earl, 1916; Wheeler, 1903, etc.); *Synchlæ callidice*, normal altitude 6,000 to 10,000 feet (Wheeler, 1903); and I have taken *Colias phicomone*, normal altitude 4,000 to 7,000 feet, and *Euphydryas cynthia*, normal altitude 5,500 to 9,000 feet. At lower levels an extent of dense forest constitutes a similar type of barrier, but one that can equally be overcome by accidental transport. Compared with such barriers, proximity within the limits of a suitable ecology is seen to differ little from overlap, and has a long-term significance that is the equivalent of contact. As such it constitutes an irrefutable indication of speciation, and if corroborated by any other data, morphological or otherwise, it is undeniable proof. The idea that proximity indicates two conspecific races kept apart, because they would blend if they met, is a theory resting entirely on negative assumption. Some hold that, in the event of overlap, a necessary attribute of speciation must be the absence of intermediates. This is an artificial distinction. A smaller or greater number of intermediates among overlapping races is just as much an indication of speciation as their absence would be; provided the parent races are present in typical form. It has been pointed out that between two species such crosses are probably accidental; between conspecific races crosses would be a more normal occurrence that would lead to the elimination of one or both races. But the question of intermediates is in itself not altogether simple. To pronounce a specimen to be an intermediate requires a knowledge of the range of variability, both superficial and morphological, in both races. At the moment we are only concerned with the superficial. As an example take the species *Pieris napi* and *P. bryoniæ*. These species have been the subjects of many breeding experiments. What may have struck some collectors was the imperfect knowledge often displayed concerning the variation, habits, and distribution of these species in nature. The two are known to fly together at Mödling near Vienna, but this is often ignored and no efforts to corroborate it in other districts have been made. Near Mallnitz in the Hohe Tauern mountains I found the summer generation of *P. napi* abundant between July 6 and 14, and with it three worn but unmistakable males of *P. bryoniæ*. There is no possibility of mistaking the males of the latter with the summer males of *P. napi*. The first generation of the latter must have been flying before the *P. bryoniæ* emerged; it therefore fills the gap between the two generations of *P. napi* and lasts into the beginning of the second. In the face of such facts, which corroborate the Vienna records, it seems pointless to question that the two are distinct. *P. bryoniæ* is said to have but one generation in the central Alps and to fly in July from about 4,500 feet upwards. I have taken it as low as 3,800 feet, and at this level it emerges in late May. Above 5,000 feet it can produce a partial second generation. I have a specimen from the Albula Valley taken on July 27, at 5,300 feet, which is a second generation, for the first occurs in that district in early June and the specimen shows the loss of markings on the underside of the hind wing that characterizes the second generation of *P. napi*. I have another similar example from the Simplon Pass taken on August 5. The first generation flies in this locality in mid June. Uncertainty also exists about the ground-colour of the females of *P. bryoniæ*. The idea that it must be yellow, though often held, bears no relation to fact. White females occur everywhere, and the range of melanic suffusion is complete on either ground-colour. It is impossible to maintain that one or two white females are *P. napi* and that all the other more melanic white females that fly with them are *P. bryoniæ*. The frequent presence of white females in the subspp. *flavescens* and *neobryoniæ* is accepted without question. The fact is that the female of the species is dimorphic in all races. Records of mixed races in the Karawankan Alps are doubtless the result of incomplete observations and mistaken identification of the white females of the subsp. *neobryoniæ* for *P. napi*. These white females are connected by a chain of colour forms to the yellow females, as also happens in the subsp. *flavescens* (see the magnificent plates given by Müller and Kautz, 1939). Enough has been said to show how incomplete observation has been on these various points in these familiar species; many references to "intermediates" rest on no surer foundation. One can add that many localities must exist where *P. napi* and *P. bryoniæ* occur in proximity, for the highest levels attained by *P. napi* overlap the lowest normal to *P. bryoniæ;* but it is a frequent source of error trying to establish distributional data on the result of a few days collecting in one district. This becomes obvious on comparing results obtained by different collectors. Several collectors, and I myself, have taken series of the nominate subspecies of *Erebia alberganus* in the Upper Engadin, yet, because they have not found it, others have denied that it exists there. Colonies of one and the same race are to be found in separate places in one district. In between the insect is not seen; but it has passed between these places to establish the colonies and still doubtless can do so at intervals. It is the same with distinct species, but colonies of different, conspecific races are not found in such proximity, for if they meet they mingle and one or other disappears. For this reason it is impossible to have intermediates between conspecific races extending over large areas. Where this is supposed to be the case, the insects must either be distinct species, or else a subspecies and a dependent "form"; the latter always shows an extreme range of variability in company with a variable percentage of the typical parental race. The "form" never exists as a pure race. Much confusion has been caused by the naming of such "forms" as "subspecies". If two colonies in proximity are not one and the same race, they can be accepted as distinct species as confidently as if actual overlap was known to occur.

MORPHOLOGY

Not only does morphology provide one of the most practical approaches to questions of speciation, but it often proves to be the most definite. Structural characters are of the most vital attributes of the species, becoming increasingly definite as species become more widely separated in time. This leads to the great divergence in structure between species of different genera and ultimately to the elimination or addition of organs. Yet structure remains completely unaffected by superficial change within a species, though such change can produce individuals of one species resembling types of two different subfamilies. This indifference to ecological influences is an irrefutible proof that structural development, which, as we have seen originates with specific nature, is correlated to the species for all time. This explains some of the strange anomalies between structure and habit that are occasionally to be seen. A good example is in birds with the most highly specialized type of foot, one capable of grasping, that have acquired the power of swimming and diving and obtain much of their sustenance below the surface of the water, a mode of existence entirely unsuited to the species-linked type of foot. A change from this type, however, could only develop with the emergence of another species. A species-linked structure can vary between one race and another to a great extent, but such variability cannot lead to the establishment of a type replacing that peculiar to the species until such time as the race has become a physiological unity, for prior to this interbreeding with other races will still be a natural act and every chance contact will check existing varietal trends and introduce others thereby increasing the possible range of variability and disrupting advance towards any predominant change in the species-linked structure. The establishment of physiological unity limits the range of variability to that existing in the race at that time; on this restricted basis, selective forces will be able to fix developing characteristics, enabling them to become predominant and ultimately permanent elements in the new species. In Lepidoptera one finds at times that a species can produce, without the slightest change in its original species-linked structure, incipient characters of a kind normal to some other species. An example of this is the presence in the genitalia of *Erebia medusa* of rudimentary teeth on the ædœagus and minute points on the penis-sheath, suggesting these features in *Erebia epipsodes*. This variation, however, in no way affects the species-linked characters of the genitalia of *E. medusa*. The *Erebia* species develop in groups of very closely-connected species. Specialization in the structural group-character gives the species-linked characters. The two species in question are members of very distinctly separated groups. This type of variation in *E. medusa* is obviously a secondary development liable to occur in any congeneric species and never a real indication of any closer relationship. One may add that the development of species in groups is to be looked for wherever extensive variability exists. Indications of such group-development are found in all large genera if they are really homogeneous.

The foregoing facts show how close is the correlation between all species-linked structural character and specific nature. So marked is this that two types of specific, structural formation cannot be reconciled in a single species. The degree of difference is of little importance so long as the types indicate two distinct lines of development. As such they are drawing apart, and their separation can only become more decisive with the passage of time. Insects are minute creatures and, obviously, structural character must be on a microscopical scale. This causes uncertainty, for many are ready to accept differences that can easily be seen, but those requiring more magnification are often suspect and frequently ignored. Yet size is immaterial; constancy the only criterion. In the perfect insect any sclerotized part can give important characters, such as the legs, genitalia, etc. In fact in insects sclerotization is of the same importance as the skeleton in vertebrates. It must be emphasized, however, that structural variability can be considerable, and the range of such normal to an organ must be established in a number of species before any attempt at specific characterization can be made. When an organ is found to display species-linked characterization in a group of species, its testimony can be accepted with confidence even though the variation in one species can approach the typical formation in some other, so long as the two extremes lie clearly apart. This has been proved by the fact that in some such cases the early stages of the two species are fully distinct.

As a matter of fact structural character existing in conspecific races is rarely (? ever) of a sufficiently distinctive quality to permit of any considerable range of variability in a single organ. It follows that in itself the presence of an extended range of variability in one organ is almost certainly an indication of speciation, and a possible variatal approach implies nothing more than an indication of past relationship. Many of these points are frequently disregarded, and one finds divergent types of structure united for arbitrary reasons. It was established that mutilation of the claspers in the male genitalia did not prevent enforced pairing (Lorković, 1952a). On the strength of this Lorković assumed that the claspers were of little value in the act of pairing and that the uncus was all important (Lorković, 1953, p. 210). He therefore maintained that the uncus alone was diagnostic of speciation and mixed different types of clasper-formation as conspecific. It has been shown, however, that the claspers do fulfill some function in pairing (Warren, 1954) and, considering both the uncus and the claspers in the Rhopalocera as a whole, one finds in many cases in the Nymphalidæ and Lycænidæ that the uncus is lost; so far as my knowledge goes no species exists in which the claspers are lost. Thus in nature it is the uncus, not the claspers, that can be dispensed with, a warning that completely artificial experiments may only give artificial results (see Warren, 1957, pp. 363, 370).

The female genitalia on the whole are of less practical value than the male. There is a basic uniformity in the sclerotized parts that inhibits response to specific influences. Extreme variability sometimes prevails, as in the genus *Erebia*, where the genital plate of the 8th sternum appears in a number of different types in every race (not species). These types reappear in different combinations in races of various species and can occur in a different ratio of frequency in different colonies of one and the same race (Warren, 1953b; 1955a). In other genera an equal degree of instability may not exist, but the knowledge that it can will always necessitate extended research before relying on a character if any marked degree of variability is present. On the other hand in some groups little variability exists, but in these specific characterization is often slight, and not infrequently between closely related species there is no recognizable difference at all. Knowledge of the female genitalia will therefore only very occasionally add in practical degree to that gained from the male.

Enough has been said to show that there is no valid reason for uniting as conspecific insects developing two distinct types of structure. Some collectors will ask at once if this statement is not disproved by the well-known case of *Pyrgus malvæ* and *P. malvoides*. The union of these species has been an arbitrary act based either on an assumed isolation or the occurrence of "intermediates" in a certain district of France. The distribution of these insects is usually summed up as never occurring together, *malvæ* a northern and *malvoides* a southern race. In actual fact *P. malvæ* has an immense distribution in Europe and Asia, while *P. malvoides* is confined to the south-west corner of Europe. *P. malvæ* occurs equally far to the south in Greece, where it develops the large and distinctly coloured subsp. *græca*. In Spain *P. malvoides* has evolved a browner race, the subsp. *pyrenaica;* only as it passes north in France and the Alps does it assume resemblance to the nominate race of *P. malvæ*. If *P. malvoides* is only a race of *P. malvæ*, why is it that when both occur in the extreme south they develop two such entirely different forms? Over a distance of about 300 miles in the central Alps they occur in very close proximity in both mountains and lowlands, and as both can ascend to about 8,000 feet there is no ecological barrier to keep them apart, and they may often meet. This is so in the Rhone Valley in Switzerland, where in one district they were only a mile or two apart thirty years ago, and as they were steadily approaching they must have met long since. Actually Sheldon years ago took a specimen of *P. malvoides* far to the west of the boundary line of *P. malvæ*. The two meet in France, and over an area of some kilometers intermediates were found in some number. This has been taken as proof that they are one species (Picard, 1948). In this case the intermediates are structural and were said to occur with such frequency that it was "difficult" to find perfectly typical specimens of either, which, however, proves that such typical examples do occur and that the hybrids are interspecific. Little exact information was given about the intermediate structural characteristics, but the uncus was said to change from the "simple" to the "bifid" type abruptly. This is confusing, for the uncus in *P. malvoides* is always bifid, the division extending for about half the total length though the two parts lie together. Nearer the tip they separate, standing apart for a short distance, but closing together again at the tip. On the other hand the processes called the "uncus" in *P. malvæ* are not a true uncus, which is a development of the entire tergum of the 10th abdominal segment, but are tergites, separated by a dorsal gap and movably articulated to the tegumen, which as Chapman noted (1919), is a characteristic unknown in any other hesperiid. A transition between such totally different dorsal processes would be an impossibility. The female genitalia are said to show transitions ranging from the typical formation of one species to that of the other, which confirms the presence of typical specimens of both species in this sex also. In such interspecific crosses it is known that perfect, intermediate structural formations are developed when homologous parts are of similar type, which I have illustrated (Warren, 1937a), and this blending of types can appear in the scales also (Kaisila, 1950, Fig. 2). In *P. malvæ* and *P. malvoides* such amalgamation could only be expected to occur in the style or antistyle, as was the case in Picard's specimens; elsewhere only abnormal formations would result. Recently the two species have been recorded flying in close proximity in a number of localities near Innsbruck, and actually together in several (Kauffmann, 1955). Out of 47 specimens Kauffmann dissected, 33 were *P. malvoides*, 12 were *P. malvæ*, and two were hybrids. The photographs he gave of the genitalia of these hybrids are remarkable in that, excepting the gnathic processes, they are absolutely typical of *P. malvoides*, even on the ventral aspect of the gnathic processes; it is only the dorso-distal part that shows abnormal development (Kauffmann, 1955, Figs. 2, 3). This is the exact reverse of Picard's records, and the fact that only two specimens out of the 47 examined were hybrids is also strikingly at variance with the French records. In this, one has a most remarkable, natural demonstration of the uncertainty of results following on interspecific crosses, which has already been mentioned and will be referred to again, and an object-lessen of the unreliability of data derived from such sources. The term "dual-species" has been used for these two insects, but this solution of the question is only supported by guesses as to the age and origin of two of the subspecies envolved; the other two (*græca* and *pyrenaica*), probably the most characteristic of the four, are ignored. Such conceptions cannot be held to be of practical help in systematic work; in the absence of full data of marked significance surmises as to what occurred in passed geological periods are valueless. The close proximity in distribution of these insects throughout the Alps is practically proof they are distinct species; the occurrence of the typical forms together with the hybrids also point to contact of two species, and the little known of the early stages gives further corroboration. There is a marked difference in the number of transverse ribs of the egg, which are known to be about twice as numerous in *P. malvæ* as in *P. malvoides*, and though the number of vertical ribs varies, the number extending to the micropylar hollow seems distinctive (Chapman, 1906; Kauffmann, 1950). Added to this is the fact that five parts of the male genitalia (uncus, gnathic processes, depth of claspers, stylifer combination, and dorsal ridge-teeth of style) are developed on distinctive lines in the two species; four of these in *P. malvæ* presenting formations unique in the genus, and the female genitalia are also distinctive. It would be difficult to imagine adequate reasons for uniting such dissimilar species; so far the data advanced for this purpose only serve to corroborate the testimony of the genitalia. But genitalic character is very frequently not so pronounced. An example of slight genitalic characterization and its value is given by many species in the genus *Colias;* here it is often so slight that it has been said not to exist. But it does and can be very conclusive (Warren, 1950). In the majority of all species of insects, a specific degree of structural individuality is present and observable. There are cases when variation seems common to two species, but there almost always is a limit to the structural variability peculiar to one, if it can be established. The extreme case when two species display an apparently identical structural formation is rare, such suspension of development being an absolute abnormality. Some supposed cases are probably but the result of disregard of slight characterization, as in the genus *Colias*.

Turning to the scales, the androconia give good characters; Chapman (1912b), illustrated this, and that paper led to the discovery of constant seasonal dimorphism in these scales (Chapman, 1914). The androconia have frequently been shown to be correlated to the specific characters of the genitalia, and it was the discovery that these scales existed in *Erebia semo* that confirmed the characters of the genitalia in that insect as of specific value (Warren, 1951). Less use has been made of the ordinary scales, owing to the variety of types that exist and the fact that they do not display the very distinctive stages of evolutionary progression that is such a marked characteristic of the androconial scale in some families. Since the discovery that the chemical flavone was present in the scale pigments in *Melanargia galathea* (Thomson, 1926), it has been pointed out that such chemical characters are helpful in systematics (Ford, 1941). This scarcely applies in speciation, for only rarely will two closely similar species be distinguished by the presence or absence of detectable anthoxanthins, which in certain cases can be present in one race and absent in another race of the same species. But apart from such unusual cases, the presence of anthoxanthins gives data of much the same value as attaches to the presence or absence of the androconial scales, but, as the chemical does not differentiate between species in which it exists, it lacks much of the taxonomic importance of the scales. There is a strange similarity in the sporadic manner in which both the androconial scales and the pigmental anthoxanthins make their appearance. The latter, though only derived from the food of the larva, are not found in all species that feed on the same plants. It is therefore assumed that it is capacity of utilisation rather than digestion of the chemical that determines their presence in the scale pigment (Ford, 1940). It had previously been suggested that as anthoxanthins in varying forms exist in plants with distinctive scents; they might supply both an aromatic body as well as a pigment-forming body to the lepidoptera, also that both these bodies are products of katabolism of a common body, for flavone is a carotenoid and hydrocarbon groups found in all botanical perfumes are oxidation products of carotene (Allan, 1937). Allan was only concerned with the chemistry of the "assembling" scents used by female moths, but there is no reason to imagine that the male scent organs may not be supplied from the same source. The sporadic appearance of the androconial scales in some species and not in others accords well with the similar type of occurrence of anthoxanthins in scale pigment; it suggests that it is the capability of utilisation and consequent production of scent that leads to the development of the androconial scale. Further similarity lies in the varying degree of presence observable both of the anthoxanthins in pigments and the numbers of androconial scales, indicating some individual limitation in the extent of utilisation in both cases.

One cannot leave the subject of morphological study without a word or two on method. The value of a character must be established before use is made of it, if by chance it is the sole character by which a species can be recognized, care must be taken to make sure that it is not also present in some other species from a different section of the genus. This is especially liable to happen in the case of characters of the female genitalia, which tend to be of a generalized nature. Some of these will serve to identify established species after the manner of superficial characters, but they cannot be accepted as specific criteria. I have described such a case in the genus *Erebia* (Warren, 1955b). An organ will often appear of strikingly different formation according to the point from which it is viewed. Seen externally and from the side the formation of some claspers appears totally different from the internal view from above. The clasper in *Erebia pandrose* is a good example; the difference was illustrated (Chapman, 1898; Warren, 1936). The external, side view only shows a portion of the organ. In interspecific comparison of structure the actual formation of an organ is the sole criterion, but this unfortunately is often completely disregarded. Another frequent source of error is seen in comparisons of length of curved processes. Such curvature is almost always affected by variation, which causes any standard of length taken from such an object to vary correspondingly. As it is scarcely possible to estimate the degree of variability of such curvature, any distinction based on the estimated length of the process is valueless as a specific character. Mere size, unless accompanied by some change in formation or orientation of a process cannot be accepted as a specific character, although all-over size is reliable when in inverse ratio to the size of the insects. It may be well to summarize the essential points in connection with the use of morphological data. (1) Individuality in structure is normal to the species in all insects; identity of structure in distinct species is rare and abnormal, sometimes the result of equally abnormal genetical phenomena. (2) Sclerotization in insects is of equal importance as the skeleton in vertebrates. (3) A character proved to be species-linked in a number of species cannot be ignored in some to suit theory. (4) The value attaching to a character is independent of its size; the microscopic is as important as the obvious, if constant. (5) Constancy applies to a total range of variability as much as to a single type. (6) An extended range of variation in one organ is an indication of speciation (to be distinguished from frequent haphazard variations occurring in all parts). (7) Size of an organ relative to its surroundings is of value if absolute and is not assumed on measures disregarding the instability of curvature. (8) All-over size can be of value if in inverse ratio to the size of two insects; such differences can be extreme, as in the small butterfly *Lysandra coridon* where the genitalia equal in size those of *Liminitis populi*. (9) It is important to examine unmounted specimens, but accurate comparison of any kind, and above all accurate measurements or photographs, must be made from mounted specimens. (10) An organ, as a character, is only of value if its true (entire) formation is considered. (11) Two constant types of structure are not compatable in one species; study in every branch of zoology proves this.

EMBRYOLOGY

Less need be said on this; the value of features of the early stages is recognized when all are distinctive. In cases where only one stage is, it is more apt to be disregarded. The egg is of value even if unsupported by the other stages, especially if of the "upright" type. Here the trouble of microscopic characters arises again, but when constant the differences are structural and have the value of such. In some species the micropylar area alone can distinguish species very clearly (Chapman, 1912a, Pl. 19, 20). The diameter of the egg can also distinguish species in some cases that show little else distinctive in the early stages: i.e., *Lysandra bellargus* 0.57 mm., *L. coridon* 0.60 mm., *L. hispana* 0.70 mm. (Chapman, 1910). Another point of value in characters derived from the egg is that they are much less liable to be affected by ecologically engendered variation. The larva can be distinctive, but colour is useless, though helpful for identification. Pattern is the most dependable character; food-specialization always needs support; apparently fixed habit can easily change. I have bred a larva of *Boarmia roboraria*, found after hibernation, entirely on hazel, yet it must have fed before hibernation on oak, the only food that it was known to eat in this country (England), though it has been recorded on birch and apple in Scandinavia. Structural details are of course helpful, such as the presence or absence of the honey-gland in some lycænids (see summary of species by Hinton, 1949). Here also Chapman gave some striking measurements of the diameter of the head in full-fed larvæ: *Maculinea arion* 0.72 mm., *Polyommatus icarus* 1.2 mm., *Lysandra coridon* 1.5 mm., *Plebejus argus* 1.00 mm., and *Cupido minimus* 0.84 mm. (Chapman 1910, p. 338). It is remarkable that in the largest species the size is the smallest. The pupa is often uniform in closely related species, but shape, proportional dimensions, and some structural details can be useful. Colour is valueless, and changes resulting on artificial conditions as recorded (Fearnehough, 1948), are no criterion for judging natural changes and have no bearing on speciation.

GENETICS

Contrary to expectations, this source has not proved to be of much practical value in questions of speciation. Some results of cross-breeding experiments have been referred to already. Fertility between hybrids varies in one and the same cross on different occasions, sometimes to a very appreciable extent. Sterility at times is known to be influenced by the individual nature of different specimens. Recent experiments in crossing *Papilio machaon* and *P. polyxenes* have given the same uncertain results. In the main the hybrids were infertile *inter se*, but some back crosses were fertile (Clarke and Shepard, 1953). Observations on *Anthrocera* species in nature, and the frequency with which five- and six-spotted species were seen to pair, led Bethune-Baker to the conclusion that in these cases mating was merely a question of which male species found the female first (1918). It has been recorded that the pairing of *Colias eurytheme* and *C. philodice* in captivity is more readily obtained when the male is *C. philodice;* but in crossing the F1 hybrids, these most frequently are sterile if the male in the original cross has been *C. philodice*, but not completely sterile when the original male has been *C. eurytheme* (Clark, 1932; Gerould, 1943). This suggests that some greater degree of pathological difficiency affects the male *C. philodice*. Experienced workers are always guarded in the interpretation of their data; others will take the first result obtained and call it proof, ignoring that the opposite is as probable. On the other hand, as Mayr has pointed out (1949), there is sometimes considerable sterility in crosses between individuals of different geographical races of one species. Further, a not infrequent occurrence in such intraspecific crosses is imperfectly sexed individuals, described by Standfuss as sexual heterozygotes (1915). It is remarkable how little attention these two last occurrences attract, though they are very significant. The frequency with which these indecisive results are encountered in both intraspecific and interspecific crosses (when closely related species are envolved) indicates how slight is the difference of genetical constitution in these stages of racial and specific evolution. It follows that really practical results bearing on speciation cannot be expected from breeding experiments except with quite mature species, the status of which is seldom in question. The statement so often made, to the effect that cross-breeding alone can determine the nature of two doubtful races, is most misleading.

The study of the chromosomes is only occasionally helpful, for equality in numbers is of course meaningless. On rare occasions the occurrence of polyploidy gives a decisive result, as in the case of the Spanish species *Erebia hispania*, separated from the alpine species *E. tyndarus* on this account (de Lesse, 1954). This, however, cannot often happen, for polyploidy is held to be an abnormal phenomena (Mayr, 1949). There is some ground for supposing such abnormality to be responsible for the equally abnormal occurrence of two species that are morphologically identical, though not always. The most obvious drawback to the value of the chromosome number for systematic purposes is that it is known the chromosome numbers can alter racially within a species and aberrationally in a race, the variation being anything from one to three chromosomes. There are of course many distinct species in which the chromosome number only differs by one and many more that all have an identical number. All the same this does not justify the attaching of a definite value to small changes in numbers unless such changes are corroborated by data from other sources. On the whole, practical help will only be obtained from the chromosomes occasionally; the results of cross-breeding will more frequently be suggestive than definite. It can, however, be accepted with fair confidence that the criteria discussed in this paper, if followed with consistency, should enable most problems of speciation, other than the primary, to be resolved.There remains a point on which official assistance would be of great value. It is evident, when considering the close identity of the subspecies and the single-race species, that the latter is but a subspecies that has become a physiological unity. Really exact estimation of what constitutes a subspecies is therefore of vital importance; only too often one finds what are merely recurring aberrations described as "subspecies". Many systematists have sought greater exactness by introducing a variety of names for the pre-specific category, all described in slightly differing terms, but applying to the same stage. Much confusion has been caused by the failure to recognize pre-racial variability for what it is. Aberrations, recurring aberrations, or forms, exist in perpetually varying proportions. I have long used the term "form" to cover such fluctuating percentages of the race; but it is immaterial what name is used to distinguish them so long as their existence is recognized as something distinct from the true subspecies. The characteristic of such "forms" is that they are factors of a subspecies, and only occur with that subspecies. The latter can exist without the form. Statistics of the degrees of presence of characters are sometimes formulated, and on their strength predominant "forms" are called "subspecies". All such "forms" vary in number in any locality from year to year, and applying the term "subspecies" to them causes different collectors to record different "subspecies" from the same locality, according to the season. A good example is given by the species *Boloria pales*. In eastern Europe the subspecies *pales* predominates; in the central Alps the form *palustris*. This variety is correctly described as *B. pales* subsp. *pales* form *palustris*. But where it predominates much confusion has been caused by referring to it as *B. pales* subsp. *palustris*, for many examples of this "subspecies" do not differ from the typical subsp. *pales*. Following on such methods one finds the describing of two, or even three, "subspecies" or "races" from a single locality or district. No amount of statistics can justify such a course which is in opposition to fact; any subspecies can develop numerous "forms" in different areas. Clearly, the first essential is an accurate definition of the term "subspecies". I have long restricted this to races that exclude all other true races (subspecies), of the same species from the area of their distribution, so far as is ascertainable; but this naturally includes all the "forms" a subspecies may develop, no matter what the proportion of their presence may be, from single specimens to 80 or 90 per cent of the colony. *For the subspecific strain still persists in all* and may increase again at any time, for there is nothing fixed about the percentages in these cases. I have formulated this idea in differing words on various occasions during the past thirty years (Warren, 1926; 1937b; 1953a). In use I can claim to have found it practical, and, though when describing new races more difficulty may be encountered in obtaining the necessary data, this is no drawback for it protects one from the error of describing fragments of a race as something distinct from the race of which they are but a part. This view has in recent years been advanced in several countries by other workers also: "a race isolated within a species" (Dobzhansky, 1941, U.S.A.); "occupying a definite distribution-area" (Kiriakoff, 1948, Belgium); a subspecies "conditioned by geographical or host isolation" (van Son, 1955, S. Africa).

SUGGESTION. I would urge that the Congress adopt an official definition of the term "subspecies", in simple words that no collector can fail to understand, to the effect that it implies a race that excludes all other true subspecies of the same species from the area of its distribution. The term "race" is to be retained as a descriptive term for reference to any category under discussion, for such a term is essential, but not for use in connection with a given classical name. There can be no doubt that some such official definition would be welcomed and followed by the majority of systematic workers.

Final Note. It must be remembered that although the criteria that have been discussed in this paper are specific attributes indicating the existence of established species, this does not imply that such attributes are primary or contributory causes of the origination of species. On the contrary they are the outcome of it; their evolution, as has been shown, depending on the pre-existence of a state of physiological speciation that alone assures the enduring isolation essential to their development. The value of such criteria in the recognition of species lies in the fact that their presence is a visible proof of the existence of that physiological unity of nature that is a fundamental element of the species.

REFERENCES

Allan, P. B. M. 1937. Some notes on assembling moths. *Ent. Rec.* 49: 119–122.

Bethune-Baker, G. T. 1918. *Zygæna trifolii, Z. filipendulæ*, etc. *Ent. Rec.* 30: 61, 62.

Chapman, T. A. 1898. A review of the genus *Erebia*, based on an examination of the male appendages. *Trans. ent. Soc. Lond.* Pt. 3: 209–239.

Chapman, T. A. 1906. Description of ovum: *P. malvæ. In* Tutt, British Butterflies 1: 231–244.

Chapman, T. A. 1910. *In* Tutt, British Butterflies 4: 63.

Chapman, T. A. 1912a. On the early stages of *Albulina pheretes. Trans. ent. Soc. Lond.* Pt. 3: 393–406.

Chapman, T. A. 1912b. An unrecognized European *Lycæna* identified as *Agriades thersites* (Boisd. MSS.) Cantener. *Trans. ent. Soc. Lond.* Pt. 4: 662–666.

Chapman, T. A. 1914. On a new form of seasonal (and heterogeneutic) dimorphism in *Agriades thersites* Cant. *Trans. ent. Soc. Lond.* Pt. 2: 309–313.

Chapman, T. A. 1919. The genus *Hesperia. Ent. Rec.* 31: 81–83.

Clark, A. H. 1932. The butterflies of the District of Columbia and vicinity. *Bull. U. S. Nat. Mus.* 157: 1–156.

Clarke, C. A., and P. M. Sheppard. 1953. Further observations on Hybrid swallowtails. *Ent. Rec.* 65: Supp. No. 9: 1–12.

Dobzhansky, T. 1941. Genetics and the origin of species. New York.

Earl, H. L. 1916. Four seasons at Martigny. *Ent. Rec.* 28: 52–58.

Fearnehough, T. D. 1948. Colour variation in pupæ of *Euphydryas aurinia. Ent. Rec.* 60: 88, 89.

Ford, E. B. 1941. Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 1. The anthoxanthins. *Proc. R. ent. Soc. Lond.* (A) 16: 65–90.

Gerould, J. G. 1943. Genetic and seasonal variations of orange wing-color in *Colias* butterflies. *Proc. Amer. Phil. Soc.* 86: 405–438.

Hinton, H. E. 1949. Myrmecophilous Lycænidæ and other Lepidoptera; a summary. *South Lond. Ent. Nat. Hist. Soc., Trans.*: 111–175.

Hovanitz, W. 1949a. Interspecific matings between *Colias eurytheme* and *Colias philodice* in wild populations. *Evolution* 3: 170–173.

Hovanitz, W. 1949b. Increased variability in populations following natural hybridization. *In* Genetics, Paleontology, and Evolution. *Princeton University Press.* pp. 339–355.

Kaisila, J. 1950. Über die vermuteten Bastarde zwischen *Colias hecla sulitelma* Aur. and *C. nastes werdanti* Zett. *Annales Ent. Fennici* 16: 112–121.

Kauffmann, G. 1950. Eine Eizucht von *Pyrgus malvoides* Elw. and Edw. *Ent. Z. Jahrg.* 60: (5, 6).

Kauffmann, G. 1955. Nochmals über *Pyrgus malvæ* L:—*malvoides* Elw. and Edw. in Nordtirol. *Mitt. Münch. ent. Gesl. Jahrg.* 44–45: 479–485.

Kiriakoff, S. G. 1948. On the so-called "lower" taxonomic categories. *Lepidopterists' News* 2: 3–4.

de Lesse, H. 1954. Recherches cytologiques et biogéographiques sur quelques Lépidoptères. *Bull. Soc. Zool. Franc.* 78: 287–291.

Lorković, Z. 1952a. Modes d'accouplement artificiels chez Lépidoptères et son application dans les recherches de la fonction de l'appareil génital chez les insectes. *Trans. 9th Int. Cong. Ent.* 1: 223–224.

Lorković, Z. 1952b. Beiträge zum Studium der Semispecies. Spezifität von *Erebia stirius* Godt. und *E. styx* Frr. *Z. Lepid.* 2: 159–176.

Lorković, Z. 1953. Specifische, Semispezifische und Rassische Differenzierung bei *Erebia tyndarus* Esp. *Trav. Inst. Biol. Experm. Acad. Yougoslave*, No. 12: 193–224.

Mayr, E. 1949. Speciation and systematics. *In:* Genetics, Paleontology and Evolution. *Princeton University Press*. pp. 281–298.

Müller, L., and H. Kautz. 1939. *Pieris bryoniæ* O. and *Pieris napi* L. *Abh. Oesterr. Ent. Ver.* 1: 1–189 (Frankfurt, a.M.)

Picard, J. 1948. *Pyrgus malvæ. Rev. franc. Lépidop.* 11: 278–283.

Pierce, F. N. 1925. A supposed hybrid *Polyommatus (coridon-hylas). Ent. Rec.* 37: 24–25.

van Son, G. 1955. A proposal for the restriction of the use of the term subspecies. *Lepidopterists' News* 9: 1–3.

Standfuss, M. 1915. Beiträge zu der Vorstehenden Arbeit von A. Schweizer über Kreuzungen von *Lymantria dispar* L. und var. *japonica* Motsch. *Mitt. Ent. Zürich u. Umgebung.* 1: 54–71.

Thomson, D. L. 1926: Pigments of butterflies wings. *Biochm. Journ.* 20: 73–75; 1026–1027.

Warren, B. C. S. 1926. Monograph of the tribe Hesperiidi. *Trans. ent. Soc. Lond.* 74: 1–170.

Warren, B. C. S. 1936. Monograph of the genus *Erebia*. Brit. Mus. Lond.

Warren, B. C. S. 1937a. On a natural hybrid in the genus *Erebia. Proc. R. ent. Soc. Lond.* (A) 12: 4–7.

Warren, B. C. S. 1937b. On the evolution of subspecies, as demonstrated by the alternation of variability existing in the subspecies of the genus *Erebia. Journ. Linn. Soc.* (Zool.) 40: 305–323.

Warren, B. C. S. 1950. Speciation in the genus *Colias. Lambillionea* 50: 90–98.

Warren, B. C. S. 1951. *Erebia semo* Gr.-Gr. A species distinct from *E. fasciata* Butler. *Entom.* 84: 73–77.
Warren, B. C. S. 1953a. Three unrecognized species of the genus *Pyrgus*. *Entom.* 86: 90–103.
Warren, B. C. S. 1953b. Problems of speciation in the genus *Erebia*. *Ent. Rec.* 65: Supp. 1–6.
Warren, B. C. S. 1955a. Notes on the species groups in the genus *Erebia*. *Entom.* 88: 28–30.
Warren, B. C. S. 1955b. *Erebia tyndarus* and allied species: the solution of some long-outstanding problems. *Entom.* 88: 227–231; 252–259.
Warren, B. C. S. 1957. Hitherto overlooked anatomical data concerning the genital structures in the Rhopalocera *Trans. R. ent. Soc. Lond.* 109 (12): 361–377.
Wheeler, G. 1903. The butterflies of Switzerland and the Alps of Central Europe. London.

Character Displacement and Species Criteria

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ABSTRACT

Character displacement is the condition of geographic variation involving two species which are relatively distinct where they occur together but tend to converge where they occur singly. This dual pattern is probably most commonly produced in the circumstance where two recently evolved, cognate species have first come into contact following the geographic isolation that mediated their divergence to species level. The active displacement processes may be reproductive, serving to reinforce the intrinsic reproductive barriers where the two species are in contact, or ecological, serving to increase their ecological differences and reduce competition. In groups where character displacement occurs, it is to be expected that the differences between sympatric species would tend to be greater than those between isolated, allopatric ones. Thus the differences between sympatric species cannot be used as a reliable yardstick to determine the status of allopatric populations considered to be on the borderline between species and subspecies.

In an earlier paper, Brown and Wilson (1956) introduced the term "character displacement" to describe the following pattern of geographic variation. Two closely related species have overlapping ranges. In the parts of the range where one species occurs alone, the populations of that species are similar to the other species and may even be very difficult to distinguish from it. In the area of overlap, where the two species occur together, the populations are more divergent and easily distinguished, i.e., they "displace" one another in one or more characters. The characters involved can be morphological, ecological, behavioral, or physiological; they are assumed to be genetically based.

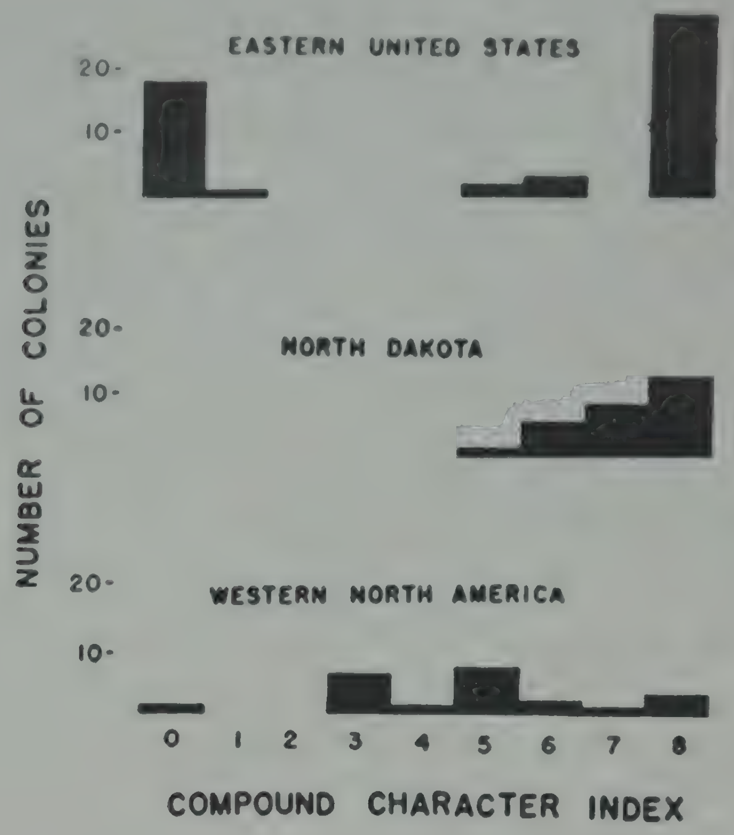
By stating the situation in two ways, we (Brown and Wilson) have called attention to the dual nature of the pattern: species populations show displacement where they occur together, and convergence where they do not. Character displacement just might in some cases represent no more than a peculiar and in a limited sense a fortuitous pattern of variation. But in our opinion it is generally much more than this; we believe that it is a common aspect of geographical speciation, arising most often as a product of the genetic and ecological interaction of two (or more) newly evolved, cognate species during their period of first contact. This thesis will be discussed in more detail in a later section.

Character displacement is not a new concept. A number of authors have described it more or less in detail, and a few have commented on its evolutionary significance. It appears to be widespread and of common occurrence in many, if not all, groups of sexually reproducing animals.

For the purposes of the present symposium I have chosen two examples of the displacement pattern from my recent revision of the ant genus *Lasius* (Wilson, 1955). The first involves multiple characters in two species of the difficult *L. flavus* group.

Where they occur together, in forested eastern North America, the related species *L. flavus* (Fabr.) and *L. nearcticus* Wheeler show differences in the following seven characters: antennal length, ommatidium number, head shape, degree of worker polymorphism, relative lengths of palpal segments, cephalic pubescence, and queen size. In western North America and the Palæarctic Region, where *nearcticus* is absent, *flavus* is convergent to it in all seven characters. In this shift, each character behaves in an independent fashion; e.g., scape length becomes exactly intermediate between that of the two eastern populations, ommatidium number increases in variability and overlaps the range of the two, and queen size changes to that of *nearcticus*. In North Dakota, at the western fringe of the *nearcticus* distribution, the *flavus* population is at an intermediate level of convergence (Fig. 1).

There is some evidence that this dual displacement-convergence pattern is associated with competition and ecological displacement between the two species. So far as is known, they have similar food requirements. But in eastern North America, where they occur together, *flavus* is mainly limited to open, dry forest with moderate to thin leaf-litter, while *nearcticus* is found primarily in moist, dense forest with thick leaf-litter. There is little information available on the western North American and Asian *flavus* populations,



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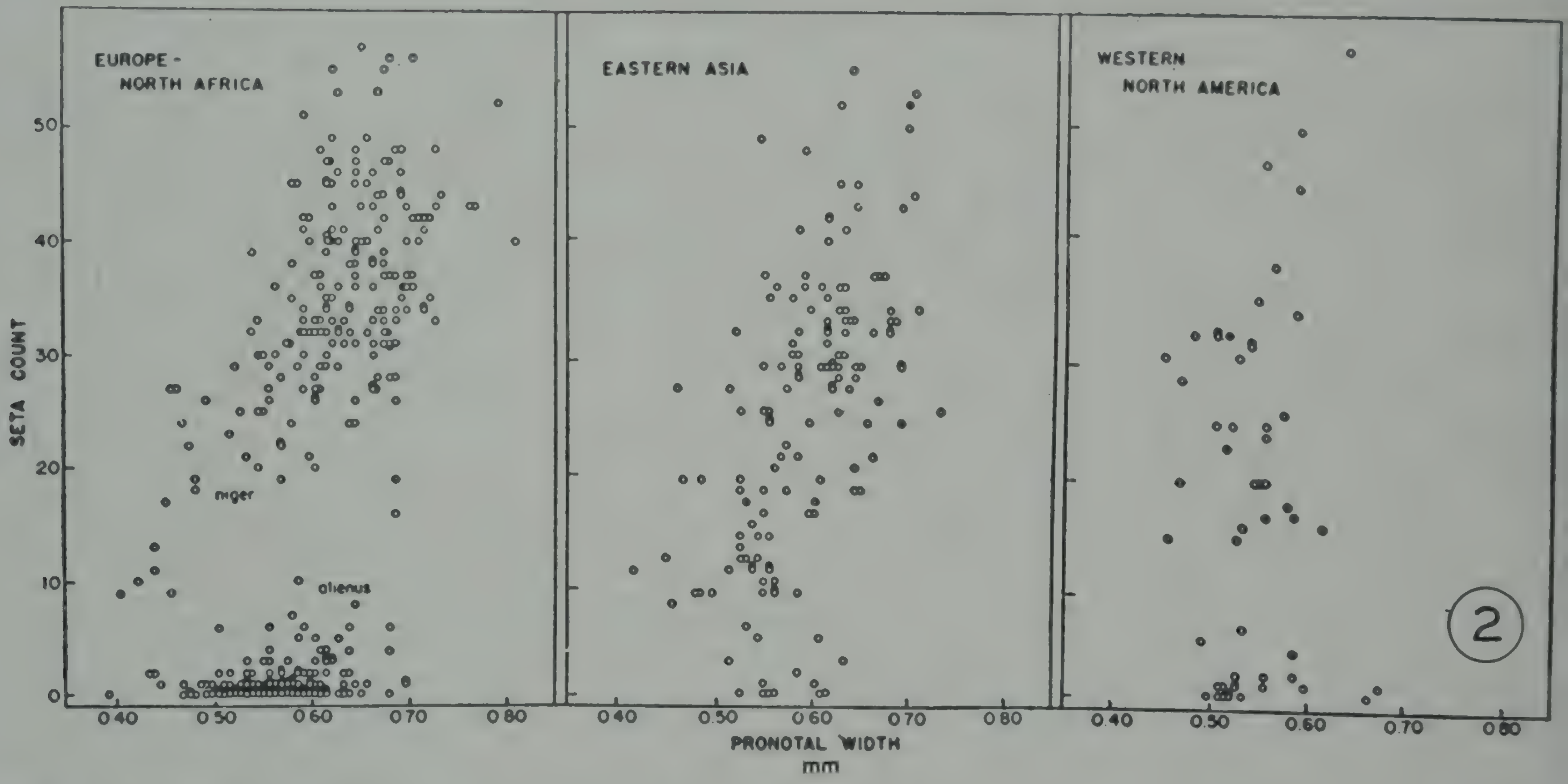

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Fig. 1. Frequency histograms of the compound character index of the ants *Lasius nearcticus* (0–1) and *L. flavus* (3–8) in three broad geographic samples. For each colony typical nearcticus characters are given a score of 0, typical eastern *flavus* characters a score of 2, and intermediate characters a score of 1. The four characters most clearcut in the eastern United States are used: maxillary palp proportions, antennal scape index, compound eye ommatidium number and head shape. Thus, completely typical *nearcticus* colonies score a total of 0 and completely typical eastern *flavus* 8, with the various ranks of intermediates falling in between (after Wilson, 1955).

Fig. 2. Pronotal width-seta count relationships in the worker caste in three geographic samples of *L. niger* and *L. alienus*. This is the principal character used to separate these two closely related species. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured. (Measurements as defined by Wilson, 1955).

but in northern Europe this species is known to be highly adaptable, preferring open situations, but also occurring commonly in moist forests.

A second case of character displacement in *Lasius* involves the two sibling species *L. niger* and *L. alienus*. The principal character used to separate these two species is the relative amounts of standing pilosity on the appendages. As can be seen in Fig. 2, the regression zones of appendage pilosity on size clearly separate the two species in Europe and North Africa, where both are dominant elements of the insect fauna. But in eastern Asia and western North America, where *L. alienus* is conspicuously less common, the regression zone of *L. niger* has shifted toward that of *alienus*, with the result that in this part of the range the two species are very difficult to separate using the pilosity character. Character displacement as I conceive it has occurred in the European and North African populations, where both species are abundant enough to interact ecologically.

Divergence between two species where they occur together, coupled with convergence where they do not, as described above in the two species pairs in *Lasius*, is a pattern that strongly suggests some form of interaction in the evolutionary history of the pair. The usual case may be one in which the members of the pair are cognate (derived from the same immediate parental population) and have recently made secondary contact following the geographical isolation that has mediated their divergence to species level. In such cases, the "terminal" populations, to which overlap does not yet extend, are not affected by the contact and remain closely similar to each other. But where contact has been made, there are two important ways in which the sympatric populations can interact to augment their initial divergence.

The first type of interaction might best be termed *reinforcement of the reproductive barriers*. It may happen that the species continue to interbreed to some extent, and either the resulting inseminations are ineffectual, or the hybrids produced are inviable or sterile, resulting in what geneticists have termed "gamete wastage." Consequently, any further ethological or genetic divergence reducing this wastage will be strongly favored by natural selection (Dobzhansky, 1951; Koopman, 1950; Kawamura, 1953).

Of conceivably equal or greater importance is the process of *ecological displacement*. It seems clear from an a priori basis that any further ecological divergence lessening competition between the overlapping populations will be favored by natural selection if it has a genetic basis (Mayr, 1949). That such a process actually occurs is suggested by abundant indirect evidence from ornithology (Lack, 1944), as well as the cases already cited above.

It seems unnecessary to go into a detailed discussion of these previously elaborated concepts, except to point out that secondary divergence of this nature inevitably entails phenotypic "characters" of the type employed in ordinary taxonomic work. Character displacement therefore may be considered as merely the aspects of such divergence that are recognizable to the taxonomist and some other favored organisms.

Since both divergent and "intermediate" populations are involved in the displacement patterns we have been describing, it is clear that the convergent populations might easily be mistaken as representing products of interspecific hybridization between the two species displacing each other. This is especially true if the convergent populations are small and isolated, or if only a single one is developed. Lack, for instance, in an early paper (1940) interpreted the Daphne and Crossman populations of *Geospiza* as being of hybrid origin, changing his mind only after he had begun to consider more fully the influence of competition on speciation (in *Darwin's Finches*, 1947). This situation adds considerable complication to the analysis of interspecific hybridization in nature, for it is clear that the alternative explanation of displacement should at least be taken into account.

Of far more importance for systematic theory, however, is the light which the conception of character displacement throws on the old problem of the status of allopatric (isolated) populations. Few authors hesitate to assign such populations either subspecific or specific rank, and most, it is hoped, appreciate the fact that their decisions are essentially arbitrary. As Mayr (1942) says, "The decision as to whether to call such forms species or subspecies is often entirely arbitrary and subjective. This is only natural, since we cannot accurately measure to what extent reproductive isolation has already evolved." There does not seem to be any definable threshold between polytypic species composed of such subspecific "units" and the superspecies composed of allopatric sister species. However, it is entirely possible that by the time an isolated population attains an ascertainable level of character concordance, it has already passed the species line; i.e., the more sharply defined an isolated subspecific population is by conventional standards, the less likely it is to be infraspecific in reality.

The phenomenon of character displacement should be borne heavily in mind in considering this matter of allopatric populations. If the present conception is correct, related sympatric species will generally show more morphological differences than similarly related allopatric ones. Hence the degree of observed difference between sympatric species cannot be considered a reliable yardstick for measuring the real status of related allopatric populations, nor can the differences among the latter be taken too seriously as indications of their relationships. In fact, the morphological standards set for determining which completely allopatric populations have reached species level may be much too strict in current practice. Despite impressions that might be gained from recent literature, many systematists have realized that in different allopatric populations (of the same species-group or genus), the degree of morphological divergence may be poorly correlated with the amount of reproductive isolation holding between them (Moore, 1954; Kawamura, 1953). In other words, where there is any question whatsoever about the objective species status of two closely related but geographically separated populations, morphology alone cannot be expected to answer it definitely.

REFERENCES

Brown, W. L., and E. O. Wilson. 1956. Character displacement. *Systematic Zoology* 5: 49–64, 6 Fig.

Dobzhansky, Th. 1951. Genetics and the origin of species. 3rd Ed. *Columbia Univ. Press.*

Kawamura, T. 1953. Studies on hybridization in amphibians. V. Physiological isolation among four *Hynobius* species. *J. Sci. Hiroshima Univ.* (B, 1) 14: 73–116.

Koopman, K. F. 1950. Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis. Evolution* 4: 135–148.

Lack, D. 1940. Evolution of the Galapagos finches. *Nature* 146: 324–327.

Lack, D. 1944. Ecological aspects of species formation in passerine birds. *Ibis* 86: 260–286.

Lack, D. 1947. Darwin's finches. *Cambridge Univ. Press.*

Mayr, E. 1942. Systematics and the origin of species. *Columbia Univ. Press.*

Mayr, E. 1949. Speciation and selection. *Proc. Amer. Phil. Soc.* 93: 514–519.

Moore, J. A. 1954. Geographic and genetic isolation in Australian amphibia. *Amer. Naturalist* 88: 65–74.

Wilson, E. O. 1955. A monographic revision of the ant genus *Lasius. Bull. Mus. Comp. Zool. Harv.* 113: 1–205, illust.

DISCUSSION

J. G. CHILLCOTT. Is it not necessary to the theory that the character changes that develop in zones of overlap be nonadaptive in all respects other than those of local separation; otherwise the variations would extend throughout the range of the species?

E. O. WILSON. Yes.

G. W. BYERS. In instances of character displacement, will not the displacement involve only one or a few characters, thus allowing the allopatric portions of the species to be separated readily?

E. O. WILSON. If you mean that some characters may vary independently of the displacement pattern to mark allopatric populations, this is possible and in fact should be expected to develop in time. We have been considering early displacement stages in which such characters play little part.

R. R. SOKAL. I am concerned over the use of the coefficient (index) of hybridization. Populations exhibiting only intermediate characters and those exhibiting a mixture of extreme characters may give identical values for the index. Perhaps this statistic should be amended to include a measure of dispersion.

E. O. WILSON. I certainly agree that this is a serious shortcoming of the hybrid (or compound character) index method of presenting data. This method should be used only as an accessory descriptive tool as it stands. If a measure of dispersion could be added, it would be a big improvement.

P. R. EHRLICH. Is it not true that in *Sitta* there are biologically significant segregates within the species that can be termed subspecies?

E. O. WILSON. In *Sitta* the characters involved in the displacement shift discordantly away from the area of overlap. Also, other characters not involved in the displacement show discordant geographic variation. Under these conditions, as in most animal populations, subspecies limits are arbitrary.

A Study of the Distribution of *Culex p. pipiens* and *Culex p. quinquefasciatus* in North America, Based on Male Genitalia (Diptera: Culicidae)

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ABSTRACT[1]

A previously described measurement of parts of the male genitalia of these two subspecies was utilized in determining their ranges. Approximately 150 lots of material contributed by culicidologists and mostly from the United States was utilized in the study. The amount of variation in the two forms was measured. The pipiens *form is found in northern North America and* quinquefasciatus *in the south; intermediate forms are common in intermediate areas. The data for these conclusions is presented in some detail, and their bearing on the taxonomy of the group is discussed.*

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[1] This paper will be published in its entirety in the *American Journal of Tropical Medicine and Hygiene.*

Species Recognition in Immature Crane Flies (Diptera: Tipulidae)

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ABSTRACT

Recent studies on the tipuline genus Dolichopeza *in North America have shown several kinds of structures in larval and pupal stages which have recognition value at the species level. Certain characters used taxonomically in the past have been found not wholly reliable. In combination with other characters, the distribution patterns of microscopic hairs on the integument of the larvae have proved to indicate species reliably. In the pupal stage, an infolding of cuticle just behind the eighth abdominal segment has been found to vary in shape, from species to species. Such characters permit species recognition among many closely related members of the same genus.*

Most previous studies of the immature stages of crane flies have dealt with single species or with only a few isolated species within a genus. Therefore, the problem of species recognition among several very closely related members of one genus has arisen only rarely, such as in the case of *Tipula oleracea*, *T. paludosa* and *T. czizeki*, which are destructive to forage crops in Europe.

The Tipulidae are a large family of insects, comprising about 8,000 species in approximately 300 genera. They are unusually widespread in distribution, occurring on virtually all the land surface of the earth, from the northern tip of Greenland to the Antaractic islands, in tropical rain-forests and in many semi-arid regions. The immature stages, while ordinarily associated with water or at least moisture, occupy a great variety of microhabitats, including earth, water (both fresh and marine), mosses, fungi, wood, and organic debris. While most species are herbivorous, others are carnivores, feeding on insects and other small organisms. As one might expect, under these circumstances, the immature stages of crane flies (as well as the adults) reflect the diversity of their habitats in a considerable diversity of form.

As a consequence, in describing the larvae or pupae of one or a few species, here and there among the thousands, earlier workers have ordinarily not been seriously pressed to find sufficient characteristics for the separation of the different kinds available to them.

Little attention has been given to intraspecific variation in larval and pupal tipulids, both because of the paucity of specimens, in most instances, and because critically comparative studies have so rarely been undertaken. Laboratory rearing of crane fly larvae to the adult stage or eggs to advanced larvae is difficult, hence the small numbers of identified immature stages available to taxonomists.

In the course of a study of the North American species of the genus *Dolichopeza*, begun a few years ago, I collected a great number of larvae and pupae from their various bryophyte habitats. Of these, some were preserved in the stage in which found, while others were placed in terraria containing mosses, in an attempt to obtain the adult insects. It was found that successful rearing most often followed collection from the natural environments of advanced, fourth instar larvae or of pupae; mortality of younger immatures was extremely high. By appropriate segregation of individuals, it was possible to obtain positively identified larval and pupal specimens. And it is these specimens and only these that can form a reliable basis for the taxonomy of immature stages. Identification of larvae or pupae on the basis of apparently related adults found in close proximity to the larval microhabitat can be very misleading. In order for there to be sound taxonomy of the immature stages, it is necessary to correlate them positively with identified adults, either by rearing them from the eggs of a known female or by keeping them alive until they reach the adult stage.

If the latter procedure is adopted, it may seem that one would have nothing but an adult fly, in the end, a specimen providing no information about its earlier forms; but such is not at all the case. It is well to save a few specimens in the whole state at each of the levels of growth, so as to have material for subsequent comparison. However, for taxonomy based upon external features, the skin of a larva or pupa is as useful as the entire individual. Thus, when the larva moults, the cast skin can be recovered by the careful observer who maintains his insects in proper isolation. When the pupa appears, the last (fourth instar) larval skin can be recovered from the bottom of the pupal burrow (in the case of *Dolichopeza* and many other genera) or from the tip of the pupal abdomen. It is a simple matter to locate pupal skins of the Tipulinae, following emergence of the adults. In the case of small Limoniinae, this whole process is much more difficult.

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[1] Contribution No. 950 from the Department of Entomology, University of Kansas.

When positively identified larvae and pupae are available in numbers sufficient to indicate the kinds and amounts of intra-species variation, the study of recognition at the specific level can be undertaken with some hope of accuracy.

In the genus *Dolichopeza*, there are fourteen species in North America. On the basis of the adults, these may be arranged in three groups, one containing a single species in a separate subgenus (*Dolichopeza* s.s.). The two remaining groups (subgenus *Oropeza*) include seven and six species respectively and appear, on the basis of external and internal morphology, to comprise very closely related forms. Ranges of these species overlap broadly, so that it is not unusual to find adults of six or eight of the species at one time, within a very limited area. Larvae of three species have been found feeding together in a single cushion of moss. This genus, therefore, would appear to present something of a challenge in the way of a study of recognition of immature forms at the species level. In attempting to solve this problem, I have worked out complete life histories (egg, early larva, late larva, pupa and reared adult) of ten species, as well as partial life histories of the others.

LARVAL CHARACTERS

Ordinarily, one encounters little difficulty in distinguishing the larvae of a particular genus from those of related genera. There is usually a sufficiency of external characters, varying greatly from genus to genus, to which reference may be made for generic identification. Thus, among North American Tipulinae, the species of *Dolichopeza* (*Oropeza*) may be at once recognized by the presence of fleshy projections, one on either side of the eighth abdominal segment, while the single species of subgenus *Dolichopeza* s.s. has a very distinctive color pattern. Other features that have been used to differentiate tipuline crane fly larvae at the generic level include the number[2] and shape of the lobes surrounding the spiracular disk, the configuration of the anal gills, body size, and shapes of antennae and other structures on the head.

The spiracular disk, with its surrounding lobes, is the most conspicuous feature of the larval tipulid. Much diversity has been found among the spiracular disks of various species of one genus, such as in *Tipula;* but the number of species of which the larval form is known represents an extremely small fraction of the total of species described in the genus. The same holds true for the other characters mentioned, throughout most tipulid genera; that is, the significance of observed variation cannot be established because too few species are known in the immature stages. Examination of the spiracular disks of the several species of North American *Dolichopeza* reveals that, while there is some variation, it does not occur within such limits, from species to species, as to be of any taxonomic utility.

Chaetotaxy has been a very attractive approach to recognition in larval crane flies, for the bristles may be single or occur in pairs, there may be small tufts of setae or patterns, or the bristles are sometimes short, sometimes long. Again, however, among the very closely related species of *Dolichopeza*, there could be found no consistent differences in size or distribution of the bristles and hairs.

In the shapes of the mandibles, mentum and hypopharynx, there are many conspicuous differences among tipuline genera and even among the species of a particular genus. It seemed at first that these characters would provide the solution to the problem of identification in *Dolichopeza* larvae, but it soon developed that only small groups of species could be distinguished on these bases. There was one further objection, from my own point of view, to the use of these structures in species recognition; to examine them, it is first necessary to dissect the larval head. And in biological studies, it is ordinarily more desirable to keep larvae alive. For this reason, the search for some useful combination of readily visible, external characteristics was pursued further.

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[2] The assertion that the spiracular disk of *Dolichopeza* s.s. is surrounded by only five lobes instead of the six found in all other tipulines has been perpetuated from an original statement to this effect by Beling in 1886, which on the basis of specimens I have examined was in error.

The solution to the problem of identification of larvae of very closely related species was found in a rather improbable character—the pattern of microscopic hairs on the integument, especially on the dorsal and pleural areas. There are two size categories into which these hairs may be divided. One includes those which, under magnification, are longer and perceptibly filiform and which often form, especially on the dorsum of the larva, transverse ridges, sometimes visible to the unaided eye as fine lines. The second category includes extremely short hairs, visible at high magnifications of the stereoscopic microscope (about 60X to 80X) and at lower magnifications apparent only as tiny spots. Quite possibly the discovery of this character of the integument came about as a result of my studying primarily larval skins instead of whole larvae, for the skins are easy to examine by transmitted light and so invite the use of the compound miscroscope, by means of which minute structures are revealed in detail. As indicated, however, high magnifications of the stereoscopic microscope are adequate for observation of these hairs on whole larvae, either preserved or living. While the following comments pertain particularly to species of *Dolichopeza*, they have been found also to apply in varying degree to larvae of other genera.

With magnification, the longer microscopic hairs may be seen to be aligned in fairly straight, transverse rows (Fig. 1) or arranged in interrupted, poorly defined rows (Fig. 2). On the thoracic and perhaps first abdominal segments and on the posterior abdominal segments, these ridges or rows of hairs often become obscured by the presence of other hairs, for which reason it has been found most reliable to base observations on segments of the mid-region of the abdomen. In certain species, the transverse rows of larger hairs are conspicuous, while in others they are only faintly indicated.

Between the rows of longer hairs on a typical abdominal segment are situated the lines of minute hairs, variously distributed according to the species. Such hairs may occur in short rows with clearly defined terminations (Fig. 3), or the rows may be relatively long, with their ends difficult to discern (Fig. 4). Within a row, the minute hairs are of uniform size in some species, but in others they are longer in the middle portion of the row, giving its ends a tapering appearance. The rows of minute hairs are sometimes rather evenly spaced betweeen the ridges of larger hairs (Fig. 3), while they are in other species crowded toward one ridge or the other, leaving a zone free of minute hairs (Fig. 4). Only the minute hairs are found on the pleural surfaces of the larva. Here, they may be arranged in small, circular patches (Figs. 1 and 2), or may occur singly or in very short lines of perhaps three or four hairs. Within the species, these distributions of both longer and minute microscopic hairs exhibit remarkable constancy and have been found wholly reliable in species determination.

PUPAL CHARACTERS

Recognition of genera of tipuline pupae has been based largely upon the configuration of the respiratory horns, cephalic crests and the sheaths of maxillary palps and antennae. Alexander (1920) lists the following characters that will prove of greatest value in the separation of the species of *Tipula*: 1, general form, whether terete or depressed; 2, mouth parts; 3, pronotal breathing horns, their relative length, size, and form; 4, armature of mesonotum; 5, wing sheaths and leg sheaths; 6, spines on abdominal segments, their size and number, whether lacking or present at base of posterior ring of sternites, arrangement and number of pleural spines; and 7, cauda, shape of genital sheaths, armature of dorsum, and ventral margin of eighth sternite.

Among such a group of closely related species as *Dolichopeza*, the first and second of these characteristics are almost uniform and thus of very little taxonomic value. The respiratory horns[3] likewise are uniform throughout the genus, although the tracheal tube connecting the spiracle to the respiratory horn was found in some species to be coiled and in others straight. There is so much similarity in the armature of the mesonotum and in the shapes, lengths, etc., of the sheaths of the wings and legs, at least in *Dolichopeza*, to render these features useless for species recognition.

Probably the most attractive characters for the identification of pupae are the many spines and lobes comprising the so-called "armature" of the abdomen. The pupa (Fig. 5) exhibits an impressive array of spines and spinous processes on the pleural and ventural surfaces especially, and also on the dorsum, to a lesser degree. Examination of series of

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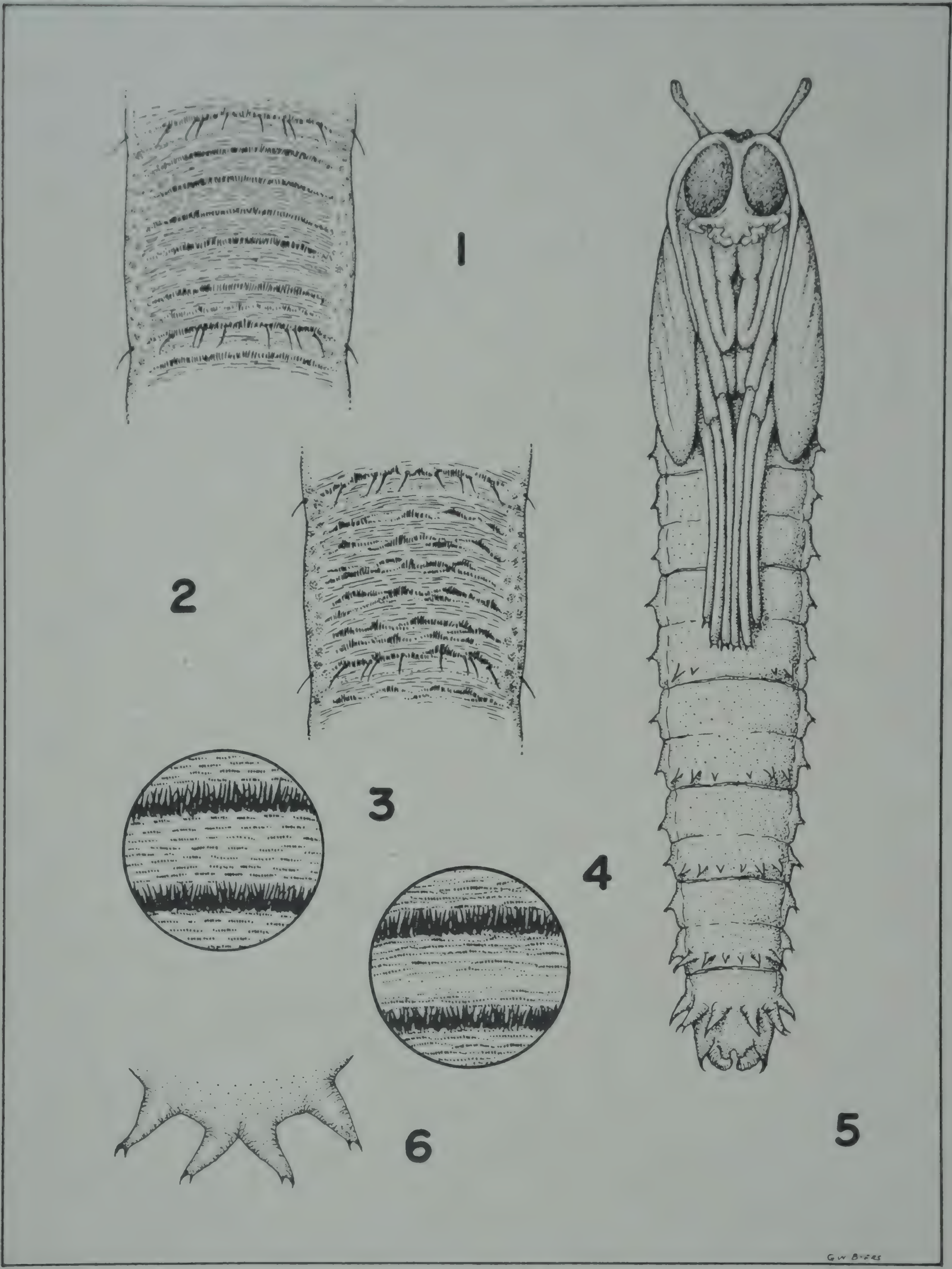
[3] The term "pronotal breathing horn" persists to the present time in crane-fly taxonomy, notwithstanding the fact that the horn is situated on the pupal mesonotum and is connected to the mesothoracic spiracle of the developing adult, within.

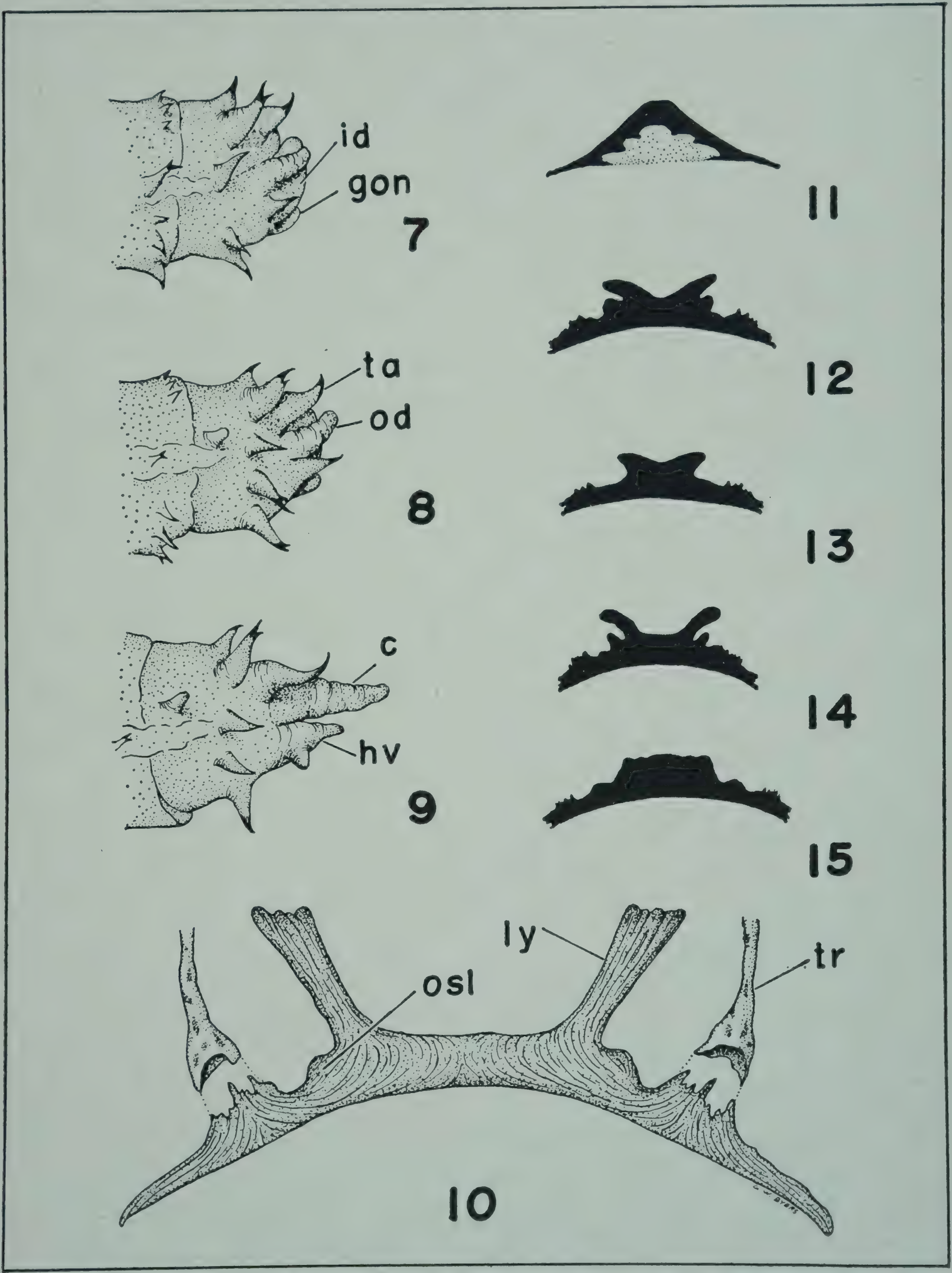


Figs. 1–6. Pupa and details of pupa and larvae of *Dolichopeza* (*Oropeza*) spp. For explanation, see text.

specimens demonstrates that the numbers and sizes of spines in the ventral rows are too variable to be reliable taxonomically. However, the pleural spines provide one useful grouping of the species of *Dolichopeza*, in that they possess either single or bifid tips. The presence or absence of ventral spines on the posterior ring of the fourth abdominal segment (Fig. 5) again allows for a separation of groups of species. While the large, spinous processes of the eighth abdominal sternite, with their conspicuous, often forked tips, offered no further taxonomic help either by their size or their shape, it was noted that in one group of species the two median processes are clearly separated (as in Fig. 5), and in the other their bases are contiguous or joined (Fig. 6).

The caudal armature proved useful only for separating at the subgeneric level. Still evident in the pupal stage of subgenus *Oropeza* are the blunt, dorso-lateral lobes of the eighth abdominal segment (Figs. 8, 9) that distinguished the larvae from other tipulines. In the males (Figs. 7, 8), the two subgenera may be separated on the basis of whether or not the sheaths of the tergal arm (ta) and outer dististyle (od) are in contact basally. There are also other, less noticeable differences.

In combination with the group-identifying characters already noted, one further feature of the pupa supplied the key to species recognition among the very similar forms



Figs. 7–15. Details of pupae of *Dolichopeza* s.s. and *Dolichopeza* (*Oropeza*) spp. Abbreviations: c—cercus, gon—gonapophysis, hv—hypovalve, id— inner dististyle, ly—lobe of spiracular yoke, od—outer dististyle, osl—outer, secondary lobe of spiracular yoke, ta—tergal arm. For further explanation, see text.

of *Dolichopeza*. This is a character never used taxonomically, heretofore, and to my knowledge never observed prior to this study.

In the larval crane fly, atmospheric oxygen enters the respiratory system through the posterior spiracles, located on the ninth abdominal tergum (the spiracular disk). When the pupal stage of development is reached, the avenue of entry for air shifts to the anterior end of the animal; that is, to the respiratory horns. During the formation of the pupa and this correlated change in respiratory arrangement, there occurs an infolding of cuticle of the tergal region of the ninth abdominal segment. This infolding occurs just posterior to the median projections of the eighth abdominal tergite, in the form of a dorso-ventrally flattened pouch, the closed end of which is directed cephalad, such that it is commonly situated close beneath the eighth tergite and may be seen through that surface. I have not followed this development in any detail, but it seems that the infolding is intimately associated with the withdrawal of the spiracular ends of the tracheal trunks. Microscopic examination of this structure reveals that tiny "stress lines" in the surrounding pupal cuticle converge into the pocket and that the remains of the larval spiracles are loosely attached to the strongly sclerotized arch formed by the converging folds of cuticle (Fig. 10). Because this pocket-like structure, formed by the cuticular infolding, when seen in dorsal aspect appears to join—or yoke—together the old spiracular ends of the tracheae, I have chosen to call it the "spiracular yoke". Not readily visible in living pupae, the spiracular yoke can be seen without difficulty in cast pupal skins, especially if they are immersed in alcohol and illuminated by transmitted light. In addition to the bowed, transverse portion with its tracheal attachments, it ordinarily bears two prominent, median lobes (Fig. 10, ly) just outside the bases of which may be smaller, secondary lobes (osl).

The spiracular yoke, in both males and females, has a characteristic shape, within limits, for each species examined, and a study of many specimens indicates that certain features of the yoke are reliably constant. Figures 11 through 15 indicate the usefulness of this character in distinguishing various species of North American *Dolichopeza*. It will be seen that the spiracular yoke of the pupa of the single species of *Dolichopeza* s.s. (Fig. 11) is strikingly different from those of pupae of the subgenus *Oropeza*. Examination of the spiracular yokes of many species of *Tipula*, *Brachypremna*, and *Megistocera* has shown that the structure is of wide occurrence among tipuline crane fly pupae and that it has a characteristic shape in each species.

REFERENCE

Alexander, C. P. 1920. The crane-flies of New York. Part II. Biology and phylogeny. *Cornell Univ. Agr. Exp. Sta. Memoir* 38. Ithaca, New York.

Nomenclatorial and Bibliographical Notes on American Bloodsucking Midges or *Culicoides*

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ABSTRACT

The author's "Catalogue of the bloodsucking midges of the Americas" (1955) included most of the literature concerning Culicoides *up to June, 1954. In the period June, 1954, to June, 1956, more than 50 articles appeared in which more than 35 new American forms are described, and these are listed. The controversial nomenclatorial problem concerning the names* guttatus Coq., diabolicus *Hoffman,* insignis *Lutz and* inamollae *Fox and Hoffman is discussed and arguments are given against various published versions of synonymy. These species are distinguished definitely by the male hypopygia, and described males are assigned to the names. Barbosa was the first to select one specimen from the type series of* insignis (Ann. Soc. Biol. Pernambuco *7: 3–30, Pl. VIII, Fig. 1b, 1947); therefore this male specimen is the lectotype. The tendency towards excessive use of neutral terms for super-specific categories in* Culicoides *is discussed, and nomenclatorial reasons are given why this practice should not continue.*

The genus *Culicoides* is of importance because it includes vicious bloodsucking pests of man, which cause severe reactions in certain individuals, and transmitters of human and animal diseases. Impelled by the needs of the Armed Forces who had to establish posts in places where these pests abound and by the modern tourist industry which demands control of these insects so that recreation areas may be developed throughout the Americas, entomologists are now devoting much attention to the group. From a genus which a decade ago had only a few workers, it has become one of the most popular, continuously attracting new students. Activity has been so great during the last few years that notable advances have been made mostly in classification but also in biology and control. Until World War II only about 60 species were known from the entire Western Hemisphere, but during the last 15 years this figure has been more than trebled. The extraordinary interest in *Culicoides* has resulted in much duplication of effort and the publication of many papers in more or less local journals throughout the Americas, with the result that many synonyms have been produced. Urgently needed therefore are catalogues and geographical lists, which include complete bibliographies, so that all workers are made aware of what has gone before, and new students have a better start when they take up the group. Building upon Vargas' excellent list of 1949, I published a catalogue (Fox, 1955b) which included 198 trivial names (involving about 160 good species) and most of the literature references to them which had been published up to June, 1954. Since that time no less than 50 articles have appeared dealing with various aspects of the subject in which more than 35 new American forms were described! These newly described forms, most of which were proposed during the period June, 1954 to June, 1956 were named as follows:

Culicoides aethionotus Wirth and Blanton, 1955b (Panama); *antunesi* Forattini, 1954b (Brazil); *bakeri* Vargas, 1954 (Mexico); *bermudensis* Williams, 1956a (Bermuda Islands); *blantoni* Vargas and Wirth, 1955 (Mexico); *bottimeri* Wirth, 1955c (Texas, U.S.A.); *camposi* Ortiz and León, 1955 (Ecuador); *carsiomelas* Wirth and Blanton, 1955a (Canal Zone); *cavaticus* Wirth and Jones, 1956 (California, U.S.A.); *dickei* Jones, 1956 (Wisconsin, U.S.A.); *dicrourus* Wirth and Blanton, 1955b (Canal Zone); *donajii* Vargas, 1954 (Mexico); *fairchildi* Wirth and Blanton, 1955a (Canal Zone); *fernandezi* Ortiz, 1954 (Venezuela); *fieldi* Wirth and Blanton, 1956a (Honduras); *flukei* Jones, 1956 (Wisconsin, U.S.A.); *footei* Wirth and Jones, 1956 (Virginia, U.S.A.); *furensoides* Williams, 1955b (Michigan, U.S.A.); *gabaldoni* Ortiz, 1954 (Venezuela); *glabellus* Wirth and Blanton, 1956a (Panama); *grahambelli* Forattini, 1956 (Panama); *imitator* Ortiz, 1953b (Venezuela); *insinuatus* Ortiz and León, 1955 (Ecuador); *limonensis* Ortiz and León, 1955 (Ecuador); *lyrinotatus* Wirth and Blanton, 1955b (Panama); *mirsae* Ortiz, 1953a (Venezuela); *neghmei* Vargas, 1955 (Mexico); *neopulicularis* Wirth, 1955c (Texas, U.S.A.); *pecosensis* Wirth, 1955c (Texas, U.S.A.); *pifanoi balsapambensis* Ortiz and León, 1955 (Ecuador); *pusilloides* Wirth and Blanton, 1955a (Panama); *rozeboomi contubernalis* Ortiz and León, 1955 (Ecuador); *ruizi* Forattini, 1954c (Brazil); *snowi* Wirth and Jones, 1956 (Virginia, U.S.A.); *sphagnumensis*

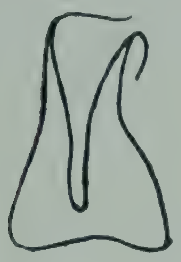
Williams, 1955b (Michigan, U.S.A.); *transferrans* Ortiz, 1953a (Venezuela); *wisconsinensis* Jones, 1956 (Wisconsin, U.S.A.).

The great increase in numbers of known species of *Culicoides* has resulted in nomenclatorial difficulties as regards superspecific designations, this being due to the desire of authors in many papers to refer to the more or less well defined groups into which the species fall. Root and Hoffman in 1937 presented an arrangement of 25 American species based upon similarities in the male hypopygia using the neutral terms "series", "intermediate form" and "group". The idea of this system was continued by Edwards (1939) who discussed the natural grouping of the males of 29 British species and has been perpetuated to an amazing degree by many subsequent authors. In an evolutionary study of speciation in the genus, Khalaf (1954) arranged the species of the world into three subgenera, subdividing them into "complexes" further subdivided into "groups" often consisting of only a few species. No brief is here made against the phylogenetic value of such terminology, but when carried over into ordinary taxonomic work, as has frequently been the case, there is a complete defeat of the main purpose of formal nomenclature in that terms are used which are confusing or meaningless. The tendency to use group names has already gone too far and should not be perpetuated for the following nomenclatorial reasons: First, it is illogical to sink in synonymy a subgeneric name yet continue to find it necessary to cite the category it represents by a neutral term; this is done by authors who refer to the "*venustus* group" although the subgeneric name Hoffmania is available. Second, the same group has been cited by different names, thus the "*venustus* group" is also called the "*guttatus* group". Third, authors are not consistent as regards sex, for example, the "*debilipalpis* group" is based on female characters although the other groups are based on the male terminalia. Fourth, authors differ in regard to what species go into what groups. Fifth, the phraseology is basically ambiguous, thus "*haematopotus* group" could mean populations in the species *haematopotus*, or a small group of species with the male hypopygia similar to that of *haematopotus*, or a much larger group of related species. Finally, no real necessity exists to have a pseudo-terminology which places little responsibility on authors telescoped into the legal one based upon carefully designed traditional rules.

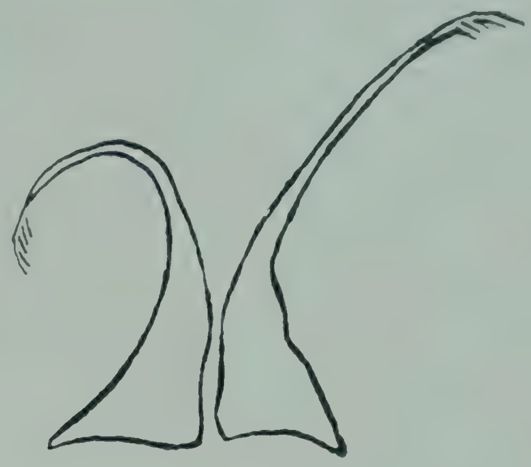
A most puzzling nomenclatorial problem is concerned with the name *Culicoides guttatus* Coq. to which a number of synonyms has been assigned by some authors. Since other authors do not agree, it is often impossible to recognize the insect to which this name applied. Notwithstanding these circumstances, the name has been used in recent years for a species coming to a light trap in Panama (Carpenter, 1951), for a possible vector of onchocerciasis in Guatemala (Gibson and Ascoli, 1952); for a species affecting rubber trees in Brazil (Warmke, 1952); for a common *Culicoides* of Florida, U.S.A. (Beck, 1952); for a species inhabiting a tidal marsh in Panama (Woke, 1954), and for a transmitter of filarial worms in Mexico (Foote and Pratt, 1954), and, with the possible exception of the Brazilian species, not one of these usages, in my opinion, is correct. Attempting to make their meaning clear, authors have used combinations of specific names such as "*guttatus* (Coquillett) (=C. *diabolicus* Hoffman)", "C. *guttatus* (and C. *insignis* Lutz)", "*filariferus* Hoffman (=*guttatus* Coquillett)", "*guttatus* (syn. C. *inamollae* Fox and Hoffman)", etc. The controversy particularly involves the application of the names *guttatus* Coq. (1904), *diabolicus* Hoffman (1925), *insignis* Lutz (1913), and *inamollae* Fox and Hoffman (1944) to zoological species, for if what these names represent can be agreed upon, others in dispute may then be disposed of.

In the subgenus to which the controversial species belong females are very similar and their characters are not sufficient to define the species. It is necessary therefor to assign males whose hypopygia offer good characters for identification to each of the species. In doing this a reasonable belief in the veracity of published observations should be exercised so that nomenclatorial and bibliographical considerations are not in conflict with zoological ones. The rule of nomenclature most applicable is that treated in the *Copenhagen Decisions on Zoological Nomenclature*, 1953, pp. 73–74, par. 137(4), and in applying this rule it seems appropriate to concede that when an author describes and figures a single specimen from a type series, he thereby has selected the lectotype of the nominal species. This interpretation of what constitutes lectotype selection applies particularly in determining to what species the name *insignis* belongs.

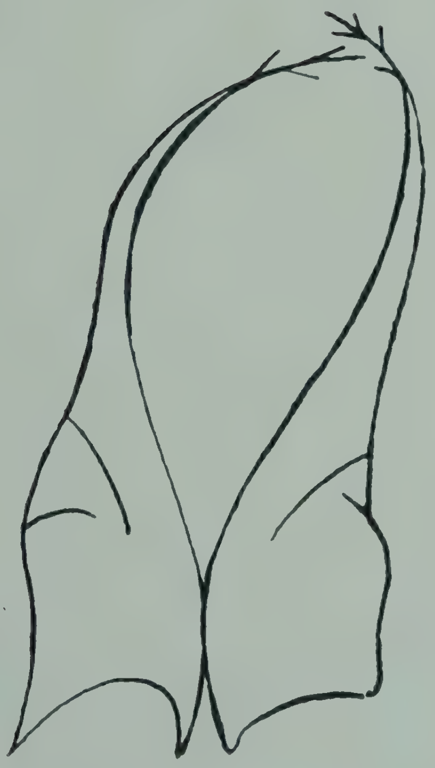
C. *insignis* was originally described by Lutz from males and females taken at Río de Janeiro and Bahia, Brazil. The description includes a figure of a female wing which looks very much like the wings of species subsequently described, particularly *inamollae* Fox and Hoffman and *flavivenula* Lutz, recently illustrated by Forattini (1954a). Certain details in the original description do not seem to apply to *inamollae*, particularly the large size, a peculiar mesonotal pattern, and the breeding place, and it is probable that *insignis* was described from more than one species. Lima (1937) studied the type material and illustrated the female palpi, but, as he did not select one specimen from the type series, his figures of several specimens can not be considered as representing a lectotype. Next to publish on type material of *insignis* was Barbosa (1947) who, in the course of revising the *Culicoides* of the Neotropical Region, found only one male in the Lutz collection and described and



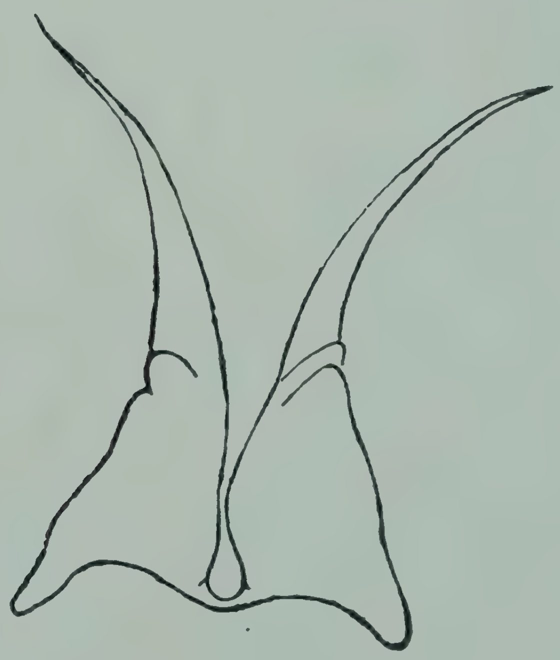
DIABOLICUS
(VARGAS, 1944)
1



INSIGNIS
(BARBOSA, 1947)
2



GUTTATUS
(BARRETTO, 1944)
3



INAMOLLAE
4

Figs. 1, 2, and 3 are the parameres of *Culicoides diabolicus* Hoffman, *C. insignis* Lutz, and *C. guttatus* Coquillett redrawn from the authors indicated to illustrate the points made in this paper; however, the original drawings should be consulted. Fig. 4, the parameres of *C. inamollae* Fox and Hoffman, from a specimen taken in a light trap at Mayagüez, Puerto Rico, in January, 1952.

figured its hypopygium. Later Barbosa wrote to Lima asking him to confirm his description, but the latter was unable to find the specimen; however, he did find others and replied as follows (Barbosa, 1952), "I am able to tell you, with absolute assurance, that the terminalia of the various males of *insignis* belonging certainly to the typical series of Lutz present aedoeagus and harpes precisely identical to those seen in Figures 1a and 1b of Plate VIII of your work of 1947". The specimen figured by Barbosa is the lectotype of *insignis* Lutz. Barbosa's illustration of the parameres of *insignis* has been redrawn in Fig. 2, and, when it is compared with the parameres of *inamollae* shown in Fig. 4, noteworthy differences are seen, in particular the presence of bushy hairs at their tips and the absence of a peculiar loop joining their bases.

C. guttatus was described by Coquillett in 1904 from three females collected by Lutz at São Paulo, Brazil. One of these syntypes was returned to Brazil where it was studied by Lima who cited it as a cotype and illustrated the wing in 1937. This specimen, presumably in the Instituto Oswaldo Cruz, is the lectotype of *guttatus*. In 1944 Barretto described the male terminalia of *guttatus* from a specimen he collected associated with females at the type locality. There is no reason why this description should not be considered to represent the male of *guttatus*. Barretto's figure of the parameres is redrawn in Fig. 3. Lima (1937) in redescribing the female of *guttatus* indicated its similarity as regards the wing pattern to *C. diabolicus*, a species described by Hoffman in 1925 from eight females collected at Cabima, Panama. Vargas (1944), pointing out the wide distribution of *diabolicus* in Central America and the Caribbean Region, described and illustrated the male terminalia from specimens taken at Chiapas, Mexico. Vargas' illustration of the parameres, which is redrawn in Fig. 1, is deemed to represent the male of *diabolicus*, for his determination was confirmed by specimens from the Canal Zone, Panama (Fox, 1948).

The several versions concerning synonymy of the four disputed species which are in the literature may be argued now as follows: (1) Lane (1949) and others believed *insignis*, *diabolicus* and *inamollae* all to be synonyms of *guttatus*, but the differences in the parameres indicate that several species are involved. (2) Macfie (1948) cited *diabolicus* as a synonym of *guttatus*, and this also is not valid on the basis of the male terminalia illustrated by Vargas and Barretto. (3) Ortiz (1950) considers *inamollae* to be a synonym of *insignis*, basing his opinion on Lutz' original description of the female and collections of *inamollae* made in Venezuela, but not on type material. Referring to Barbosa's figure of the male of *insignis*, he states that probably the male of *guttatus* was involved although the label said *insignis*. However, Barbosa's specimen is considered to be the lectotype of *insignis*, and, if it is *guttatus*, then the name *insignis* falls as a synonym of *guttatus*. (4) I believe all four names to represent distinct species on the basis of differences in the male terminalia (Fox, 1955b). A new study of the type material of *insignis*, unless it includes Barbosa's specimen, will not resolve the problem of whether *inamollae* is its synonym. Even if *inamollae* is found in the Lutz collection, nothing is proved for Barbosa selected the lectotype when he figured a male from the type series of *insignis*. It is possible that in the Brazilian fauna there occurs a species which corresponds to Barbosa's figure, and, until this is disproved, the name *insignis* should not be used. If, after the *Culicoides* of Brazil are thoroughly known, it is evident that no species has a hypopygium like that figured by Barbosa, then the name *insignis* should fall as a synonym of *guttatus*, for the parameres in Barbosa's figure, being separate and hairy at the tips, are much more similar to those of *guttatus* than to those of *inamollae*.

REFERENCES[1]

Aréan, V. M., and I. Fox. 1955. Dermal alterations in severe reaction to the bite of the sandfly, *Culicoides furens*. *Amer. Jour. Clin. Path.* 25: 1359–1366.

Blanton, F. S., O. H. Graham, and C. M. Keenan. 1955. Notes on *Culicoides furens* (Poey) at Fort Kobbe, Canal Zone. *Mosquito News* 15: 13–18.

Bruijning, C. F. A. 1956. The occurrence of some insect-borne diseases in Suriname in relation to the distribution of their vectors. Abstract in *Proc. Tenth Int. Congr. Ent.* (In press).

Coher, E. I., W. W. Wirth, and H. Knutson. 1955. *Culicoides* of New England (Diptera: Heleidae). *Mosquito News* 15: 153–155.

Downes, J. A. 1954. Observations on the swarming flight and mating of *Culicoides*. *Trans. R. Ent. Soc. London* 106: 213–236.

Downes, J. A. 1956a. The genus *Culicoides* (Diptera: Ceratopogonidae) in Canada; an introductory review. *Proc. Tenth Int. Congr. Ent.* (In press).

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[1] The following citations are those which for the most part appeared from June, 1954, through June, 1956. Other references cited in the text will be found in the author's catalogue (Fox, 1955b).

Downes, J. A. 1956b. Assembly and mating in the Nematocera. *Proc. Tenth Int. Congr. Ent.* (In press).

Duke, B. O. L. 1954. The uptake of the microfilariae of *Acanthocheilonema streptocerca* by *Culicoides grahamii* and their subsequent development. *Ann. Trop. Med. and Parasit.* 48: 416–420.

Duke, B. O. L. 1956. The intake of the microfilariae of *Acanthocheilonema perstans* by *Culicoides grahamii* and *C. inornatipennis*, and their subsequent development. *Ann. Trop. Med. Parasit.* 50: 32–38.

MacNay, C. G., 1956 (1955). Biting midges. *Ann. Rep. Ent. Soc. Ontario* 86: 121.

Fallis, A. M. 1956. Sandflies (Ceratopogonidae) as intermediate hosts for *Haemoproteus* of ducks. Abstract in *Proc. Tenth Int. Congr. Ent.* (In press).

Forattini, O. P. 1953. O *Culicoides trinidadensis* Hoffman 1925 (Diptera, Ceratopogonidae). *Arq. Fac. Hig. Saude Pub. Univ. São Paulo* 7: 123–126.

Forattini, O. P. 1954a. Redescrição de *Culicoides flavivenula* Costa Lima, 1937 (Diptera, Ceratopogonidae). *Rev. Brasil Ent.* 1: 135–138.

Forattini, O. P. 1954b. Nova espécie de *Culicoides* (Diptera, Ceratopogonidae) do Estado de Goiaz, Brasil. *Folia Clin. et Biolog.* 21: 315–319.

Forattini, O. P. 1954c. Nova espécie de *Culicoides* (Diptera, Ceratopogonidae) do Brasil Central. *Arq. Fac. Hig. Saude Pub. Univ. São Paulo* 8: 189–192.

Forattini, O. P. 1956. A new *Culicoides* from Panama. *Proc. Ent. Soc. Washington* 58: 35–36.

Fox, I. 1955a. Nuevos adelantos en el estudio del género *Culicoides*. *Bol. Lab. Clínica "Luis Razetti"* 16: 635–639.

Fox, I. 1955b. A catalogue of the bloodsucking midges of the Americas (*Culicoides, Leptoconops*, and *Lasiohelea*) with keys to the subgenera and Nearctic species, a geographic index, and bibliography. *Jour. Agric. Univ. Puerto Rico* 39: 214–285.

Fox, I. 1955c. The sandfly (*Culicoides*) problem in Puerto Rico. *Rev. Assoc. Salud Pub. Puerto Rico* 1: 31–33.

Frohne, W. C., and D. A. Sleeper. 1951. Reconnaissance of mosquitoes, punkies and blackflies in southeast Alaska. *Mosquito News* 11: 209–213.

Gad, A. M. 1951. The head-capsule and mouth-parts of the Ceratopogonidae (Diptera: Nematocera). *Bull. Soc. Fouad 1er Ent.* 35: 17–75.

Huttel, W. and N. 1955. Les Cératopogonides à travers les âges et les continents. *Acta Tropica.* 12: 123–135.

Johnson, C. W. 1925. Fauna of New England. 15. List of the Diptera or two-winged flies. *Boston Soc. Nat. Hist. Occas. Papers* 7: 1–326.

Jones, R. H. 1956. New species of *Culicoides* from Wisconsin. *Proc. Ent. Soc. Washington* 58: 25–33.

Keller, J. C., G. C. Labrecque, and R. L. Goulding. 1954. Tests with heptachlor and dieldrin for the control of sand fly larvae. *Rep. Ann. Mtg. Florida Anti-Mosquito Assoc.* 25: 95–99.

McGuire, J. U., and W. W. Wirth. 1956. The discriminant function in taxonomic research. *Proc. Tenth Int. Congr. Ent.* (In press).

Megahed, M. M. 1956. A culture method for *Culicoides nubeculosus* (Meigen) (Diptera: Ceratopogonidae) in the laboratory, with notes on the biology. *Bull. Ent. Res.* 47: 107–114.

Mirsa, A. 1954. Sobre la biología de algunos Flebotomos (Díptera Psychodidae) y datos sobre otros hematófagos colectados en Altagracia de Orituco (Estado Guarico, Venezuela). *Rev. San. Asist. Soc.* 19: 189–196.

Mirsa, M. 1954. Insectos de interés médico en "Los Chorros", Estado Miranda con referencia especial a los dípteros del género *Culicoides* Latreille (Nematocera, Ceratopogonidae). *Rev. San. Asist. Soc.* 19: 139–172.

Nicholas, W. L., and W. E. Kershaw. 1954. Studies on the intake of microfilariae by their insect vectors, their survival, and their effect on the survival of their vectors. III.—The intake of the microfilariae of *Acanthocheilonema perstans* by *Culicoides austeni* and *C. grahamii*. *Ann. Trop. Med. and Parasit.* 48: 201–206.

Ortiz, I. 1953a. Nueva contribución al conocimiento de los caracteres morfológicos externos de las hembras americanas del género *Culicoides* Ltr. (Diptera, Ceratopogonidae) con una espermateca. *Rev. San. Asist. Soc.* 18: 797–806.

Ortiz, I. 1953b. Sobre una nueva especie del género *Culicoides* (Diptera, Ceratopogonidae) próxima de *C. horticola* Lutz. 1913. *Rev. San. Asist. Soc.* 18: 807–812.

Ortiz, I. 1954. Sobre dos nuevos dípteros haematofagos del género *Culicoides* (Nematocera, Ceratopogonidae). *Archiv. Venezol. Patol. Trop. y Parasit. Méd.* 2: 221–226.

Ortiz, I., and L. A. León. 1955. Los *Culicoides* (Diptera: Ceratopogonidae) de la República del Ecuador. *Bol. Inform. Cientif. Nac. (Ecuador)* No. 67: 564–596.

Pickard, E., and W. E. Snow. 1955. Light trap collections of punkies (Family Heleidae, Genus *Culicoides*) McMinn County, Tennessee, April—September, 1952. *Jour. Tenn. Acad. Sci.* 30: 15–18.

Porter, J. E. 1956. Some effects of screens and screen treatments in retarding the entry of the salt-marsh sandfly, *Culicoides furens* (Poey). (Read at the Twelfth Ann. Mtg. American Mosquito Cont. Assoc., Beaumont, Texas).

Price, D. A., and W. T. Hardy. 1954. Isolation of the bluetongue virus from Texas sheep—*Culicoides* shown to be a vector. *Jour. Amer. Vet. Med. Assoc.* 124: 255–258.

Riek, R. F. 1953. Allergic dermatitis of the horse. *Proc. XV Cong. Int. Vet. Part I*: 664–669; *Part II*: 316–317.

Riek, R. F. 1954. Studies on allergic dermatitis (Queensland itch) of the horse. The aetiology of the disease. *Australian Jour. Agric. Res.* 5: 109–129.

Riek, R. F. 1955. Studies on allergic dermatitis (Queensland itch) of the horse: the origin and significance of histamine in the blood and its distribution in the tissues. *Australian Jour. Agric. Res.* 6: 161–170.

Snow, W. E. 1955. Feeding activities of some bloodsucking Diptera with reference to vertical distribution in bottomland forest. *Ann. Ent. Soc. America* 48: 512–521.

Snow, W. E., and E. Pickard. 1954. Observations on the seasonal activity of some night-biting Diptera. *Jour. Tennessee Acad. Sci.* 29: 17–22.

Vargas, L. 1954. Dos nuevas especies de *Culicoides* mexicanos (Diptera, Heleidae). *Rev. Inst. Salub. Enferm. Trop.* 14: 25–30.

Vargas, L. 1955. *Culicoides neghmei* n. sp. *Bol. Lab. Clínica "Luis Razzetti"* 16: 673–675.

Vargas, L., and W. W. Wirth. 1955. *Culicoides blantoni* n. sp. (Diptera, Heleidae). *Rev. Inst. Salub. y Enferm. Trop.* 15: 33–35.

Williams, R. W. 1955a. Studies on the *Culicoides* of Baker County, Georgia (Diptera, Heleidae). I. Preliminary survey and observations. *Ann. Ent. Soc. America* 48: 30–34.

Williams, R. W. 1955b. Two new species of *Culicoides* from Cheboygan County, Michigan (Diptera, Heleidae). *Proc. Ent. Soc. Washington* 57: 269–274.

Williams, R. W. 1955c. Observations on the bionomics of some *Culicoides* of Cheboygan County, Michigan (Diptera, Heleidae). *Bull. Brooklyn Ent. Soc.* 50: 113–120.

Williams, R. W. 1956a. The biting midges of the genus *Culicoides* found in the Bermuda Islands (Diptera, Heleidae). I. A description of *C. bermudensis* n. sp. with a key to the local fauna. *Jour. Parasit.* 42: 297–300.

Williams, R. W. 1956b. The biting midges of the genus *Culicoides* in the Bermuda Islands (Diptera: Heleidae). II. A study of their breeding habitats and geographical distribution. *Jour. Parasit.* 42: 300–305.

Wirth, W. W. 1955a. Report on a collection of biting midges of the genus *Culicoides* from Guatemala (Diptera: Heleidae). *Proc. Ent. Soc. Washington* 57: 109–117.

Wirth, W. W. 1955b. The biting midge genera *Psychophaena* and *Tetraphora* of Philippi 1865 (Diptera Heleidae). *Rev. Chilena de Ent.* 4: 233–235.

Wirth, W. W. 1955c. Three new species of *Culicoides* from Texas (Diptera: Heleidae). *Jour. Washington Acad. Sci.* 45: 355–359.

Wirth, W. W., and F. S. Blanton. 1955a. Studies in Panama *Culicoides* (Diptera, Heleidae). IV. Description of three new species. *Bull. Brooklyn Ent. Soc.* 50: 100–106.

Wirth, W. W., and F. S. Blanton. 1955b. Studies in Panama *Culicoides* (Diptera, Heleidae). V. Descriptions of three new species of the subgenus *Oecacta* Poey. *Bull. Brooklyn Ent. Soc.* 50: 121–127.

Wirth, W. W., and F. S. Blanton. 1956a. Studies in Panama *Culicoides* (Diptera, Heleidae). IX. Two new species related to *leoni* Barbosa and *reevesi* Wirth. *Bull. Brooklyn Ent. Soc.* 51: 45–52.

Wirth, W. W., and F. S. Blanton. 1956b. Studies in Panama *Culicoides* (Diptera: Heleidae), VI. The *hylas* group of the subgenus *Hoffmania*. *Jour. Washington Acad. Sci.* 46: 95–99.

Wirth, W. W., and R. H. Jones. 1956. Three new North American species of tree-hole *Culicoides* (Diptera, Heleidae). *Proc. Ent. Soc. Washington* 58: 161–168.

DISCUSSION

C. W. SABROSKY. Lectotype recognition is critical here. I disagree completely that a specimen not so labeled and not so designated in publication can be considered an established lectotype. Mere figuring, without designation, is not sufficient. We must rigidly construe this.

I. FOX. The authors referred to obviously intended to describe and figure the type of the species, although they may not have used the precise term lectotype.

Mycetophilidae, Chiefly from Argentina

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ABSTRACT

In the present report, 108 species are recorded for Argentina. Of these, 12 species are described as new. Keys are presented for the following subgenera: Keroplatus *s. str.*, Cerotelion, *and* Neoplatyura. *Four species, found in the Chilean center of dispersal and endemism, were found extending their range into northern Argentina.*

Through the kindness of Dr. Martin L. Aczél, we received a large collection of *Mycetophilidae* belonging to the Instituto Miguelo Lillo, Tucumán, Argentina. Later our friend Dr. J. P. Duret, from Buenos Aires, Argentina, kindly loaned us his personal collection of flies of this family. With the material which we had already obtained from various sources and the above mentioned collections, a study was made of the Argentinian species, and it was also found expedient to include also some species from Chile and Paraguay.

Difficulties were encountered in the determination of the material due chiefly to the fact that species of the Chilean subregion occurred in Northern Argentina. With the help given by Dr. Paul Freeman of the British Museum (Natural History) and of his excellent treatment of this family in "Diptera of Patagonia and South Chile", together with determined material in our own collections, such difficulties were surmounted.

As can be seen, the number of species now catalogued for Argentina surpass by far all previous records. We have, however, no doubt that many more species are still to be found and also believe that the same holds true to the Neotropical region as a whole.

Names of Brazilian tribes of Indians were used, in a few cases, for our choice of specific names. The numbers mentioned are those of the entomological collections of the "Departamento de Parasitologia da Faculdade de Higiene e Saúde Pública da Universidade de S. Paulo, Brazil".

We record one hundred and eight species, of which twelve are described as new. Keys were prepared for *Keroplatus* s. str., the subgenus *Cerotelion*, and the subgenus *Neoplatyura*.

The author takes pleasure in thanking all the above mentioned gentlemen for their help in the preparation of this paper and Mr. E. B. Ferraz of our Faculty for drawing the illustrations. All drawings were made with the aid of a 'camera lucida'

SUBFAMILY DITOMYIINAE

Only the genus *Australosymmerus* is represented in the material examined.

Australosymmerus bivittatus (Freeman, 1951)

1951. *Australomyia* Freeman, Dipt. Pat. & S. Chile, 3: 9.

Distribution. Two specimens. Terr. Neuquen, Pucará, Parque Nacional Lanin, XI. 1953. (Schajovskoi col.).

Australosymmerus insolitus (Walker, 1837)

1837. *Platyura* Walker, Trans. Lon. Soc. London, 17: 335.
1909. Johannsen, Gen. Ins., 92: 23.
1921. *Centrocnemis* Edwards, An. & Mag. N.H., (9), 7: 435.
1951. *Australomyia* Freeman, Dipt. Pat. & S. Chile, 3: 9.

Distribution. One specimen. Terr. Santa Cruz, Lago Argentino, II. 1950 (Willink col.).

Australosymmerus stigmaticus (Philippi, 1865)

1865. *Centrocnemis* Philippi, Verh. zool. bot. Ges. Wien. 15: 619.
1909. *Symmerus* Johannsen, Gen. Ins., 93: 12.
1951. *Australomyia* Freeman, Dipt. Pat. & S. Chile, 3: 8.

Distribution. One specimen Terr. Neuquen, Pucará, Parque Nacional Lanin, XI. 1953 (Schajovskoi col.); one specimen Tierra del Fuego, III. 1948 (Budin col.).

Australosymmerus tupi (Lane, 1946)

1946. *Centrocnemis* Lane, Rev. Ent., 17: 341.

Two specimens doubtfully determined as this species.

DISTRIBUTION. Prov. Misiones, Cataratas, Oberá, X. 1948 (J. P. Duret col.).

SUBFAMILY MANOTINAE

Manota palpalis Lane, 1948

DISTRIBUTION. One specimen. Prov. Misiones, Alba Pose, III. 1951 (J. P. Duret col.).

SUBFAMILY KEROPLATINAE

All Neotropical genera are represented in this collection.

Heteropterna trileuca Edwards, 1940

1940. Edwards, Rev. Ent., 11: 447; 1948 Lane, ibd., 19: 447.

DISTRIBUTION. One specimen. Prov. Misiones, Aristobulo del Valle, II. 1951 (J. P. Duret col.).

Platyroptilon miersi Westwood, 1849

1849. Westwood, Trans. Ent. Soc. London, 5: 231; 1881 Westwood, ibd., 384.
1902. Kertesz, Cat. Dipt., 1: 53.
1909. Johannsen, Gen. Ins., 17.
1934. Edwards, Rev. Ent., 4: 360.

DISTRIBUTION. Two specimens. Prov. Misiones, Deseado, XII. 1951; Prov. Tucumán, Acheral, XII. 1949 (J. P. Duret col.).

Macrocera perpictula Edwards, 1940

1940. *Macrocera* Edwards, Rev. Ent., 11: 445.

Except for slight differences in the markings at apex of wing, the single specimen agrees with the original description.

DISTRIBUTION. Prov. Misiones, Cerro Azul, V. 1949 (J. P. Duret col.).

Macrocera plaumanni Edwards, 1940

1940. *Macrocera* Edwards, Rev. Ent., 11: 445; 1950 Lane, Dusenia, 1: 35.

The mesonotal and wing markings are darker in some specimens.

DISTRIBUTION. Four specimens. Prov. Misiones, Bemberg, X. 1948; Prov. Corrientes, Mercedes, V. 1951 (J. P. Duret col.); Prov. Tucumán, La Angostura, Tafí del Valle, II. 1953 (M. Aczél col.).

Macrocera shannoni Lane, 1946

1946. Lane, Rev. Ent., 17: 344.

A series of nine specimens. A female from Cherém, State of Rio de Janeiro, BRAZIL, is here selected as the allotype of this species. There is variation as to the colour of mesonotum and wing.

FEMALE. Similar to male but both mesonotal and wing markings much stronger and distinct, specially three mesonotal stripes. Cerci small, rounded and dull black.

TYPE. Allotype female; registered under n. 10.385.

TYPE LOCALITY. BRAZIL, State of Rio de Janeiro, Cherém, VIII. 1953 (J. P. Duret col.).

ADDITIONAL DISTRIBUTION. BRAZIL, State of S. Paulo, Ribeirão Preto, VI. 1953; State of Pará, rio Mojú, VIII. 1953; ARGENTINA, Prov. Misiones, Iguazú, XI. 1953 (J. P. Duret col.).

Macrocera unidens Edwards, 1931

1931. *Macrocera* Edwards, An. & Mag. N.H., 10 (7): 255.

DISTRIBUTION. One specimen. ARGENTINA, N.O. 125 (J. P. Duret col.).

SUBGENUS KEROPLATUS S. STR.

As our previous key only included three species (Lane, 1948), and as since then we have been able to see *K. fiebrigi* Edwards, 1934, and to describe *K. caribai* Lane, 1950, and have also found another species described here as new, we do not think it amiss to include a key for species known at present.

Key for Neotropical adults of *Keroplatus* s. str.

1. With only two ocelli 2
With three ocelli; haltere with white stem and black knob; fore coxa darkened at apex; abdomen with yellowish tergites bearing basolateral dark brown markings on tergites II to VI . . *townsendi* Lane, 1948

2. Haltere with white stem and blackish knob 3
Haltere whitish; fore coxa yellowish; mid and hind femora darkened only at base . . . . *mexicana* Lane, 1948

3. Fore coxa with dark marks 4
Fore coxa yellowish; wing with three dark spots; abdomen dark brown, a longitudinal yellowish line on tergites I to IV; posterolateral margins of tergites II to apex yellowish . . . . *caribai* Lane, 1950

4. Antenna dark brown; fore coxa with apical portion darkened; wing with only two dark spots; abdomen dark brown, segments II to V with posterolateral yellow markings . . . . *fiebrigi* Edwards, 1934
Antenna with flagellar segments I to V mostly yellow, the rest dark; fore coxa with two apical rounded blackish spots; abdomen with the posterior marks on segments II to V forming bands . . *golbachi*, n. sp.

Keroplatus (*Keroplatus*) *fiebrigi* Edwards, 1934

1934. *Ceroplatus* Edwards, Rev. Ent. 4: 357.

We have a male specimen which agrees with the original description except that the wing markings, which show the mesial spots, are slightly larger than the apical one. Mesonotal markings are quite distinct in our specimen and show a brown colour traversed longitudinally by four stripes, the externals being broadest while there is also an additional indistinct mesial line.

Distribution. A single specimen. Prov. Misiones, Deseado, 20. III. 1951 (J. P. Duret col.).

Keroplatus (*Keroplatus*) *golbachi* n. sp.

Male. Head: Mouth parts very small and whitish. Palpus one segmented, the segment large, whitish. Frons yellowish-white, narrow, Antenna with broad, flat scape and torus which are yellowish but externally blackish; flagellum very much flattened, the segments broad and short; I yellow with a basal blackish mark, II to V yellowish, remaining segments dark brown. Occiput yellowish with two dilute dark brown marks behind ocellar callus, hairs blackish; ocellar callus blackish, the two ocelli inserted on each side.

Thorax: Posterior pronotum yellow. Mesonotum yellowish brown with the following blackish stripes; two diagonal lines from front and uniting into a V when the scutellum is reached, between these a slender blackish stripe which coalesces with the diagonal lines behind; two broad blackish lines on sides from anterior margin, reaching scutellum but leaving a yellow margin below, up to base of wing. Scutellum yellowish white with a narrow mesial blackish line. Pleura blackish but spiracular sclerite yellowish, upper portion of katepisternite and pteropleurite yellowish and pleurotergite broadly whitish in the middle.

Wing hyaline with the following diluted dark markings:—first small and in middle of vein R. 1; second where R. 4 reaches R. 1 while the third is more like an apical shade. Haltere with white stem and black knob.

Legs: Coxae yellow but fore one with a rounded external black spot below middle and an internal anterior one at apex; mid coxa with apical third blackish while the hind coxa has nearly the apical half blackened. Fore legs (missing). Mid and hind femora yellow with base and apex blackish, more so on hind one. Tibiae with regular rows of blackish setulae. Tarsi blackish but with extreme apex whitish.

Abdomen blackish, segments II to V with large apical yellow marks which unite dorsally forming bands. Sternite I black, II to V yellowish with black spots; rest of segments blackish.

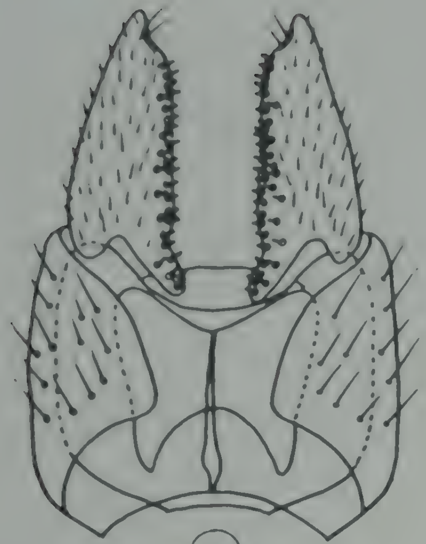
Genitalia: (Fig. 1). Basistyles with lobes fused, nearly quadrate. Dististyle longer than basistyle, triangularly shaped, with many rows of blunt differentiated and short spines over nearly the whole internal margin. Other structures as in the figure.

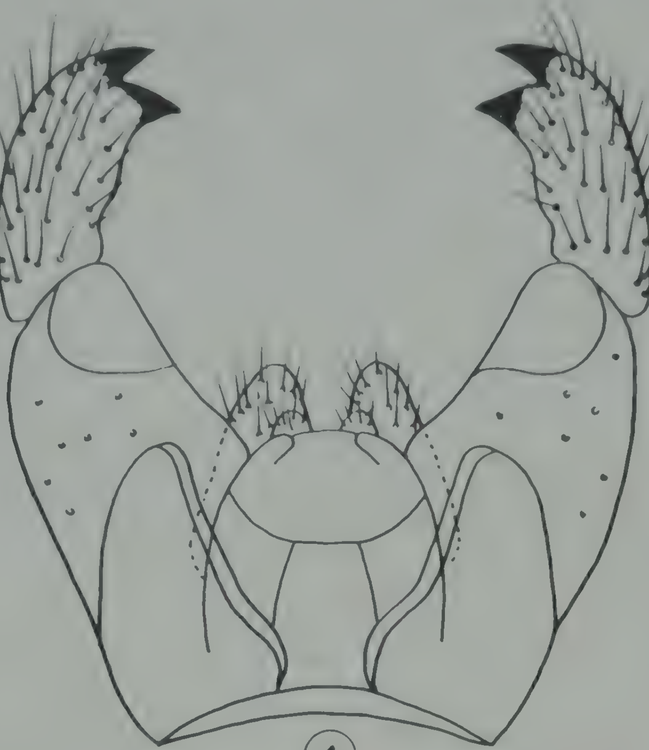
Female: Unknown.

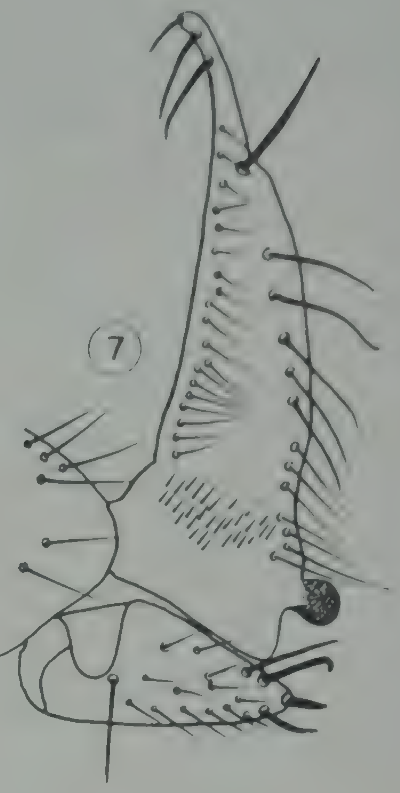
Type. Holotype male. To be returned to the Institute Mihuel Lillo, Prov. de Tucumán, Argentina.

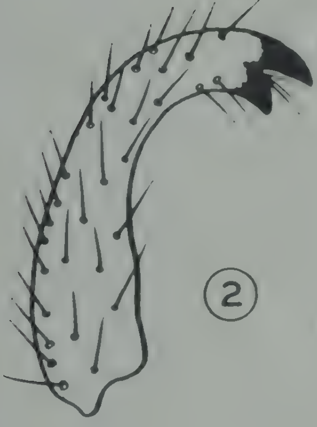
Type locality. Prov. de Salta, Urundel, II. 1950 (R. Golbach col.).

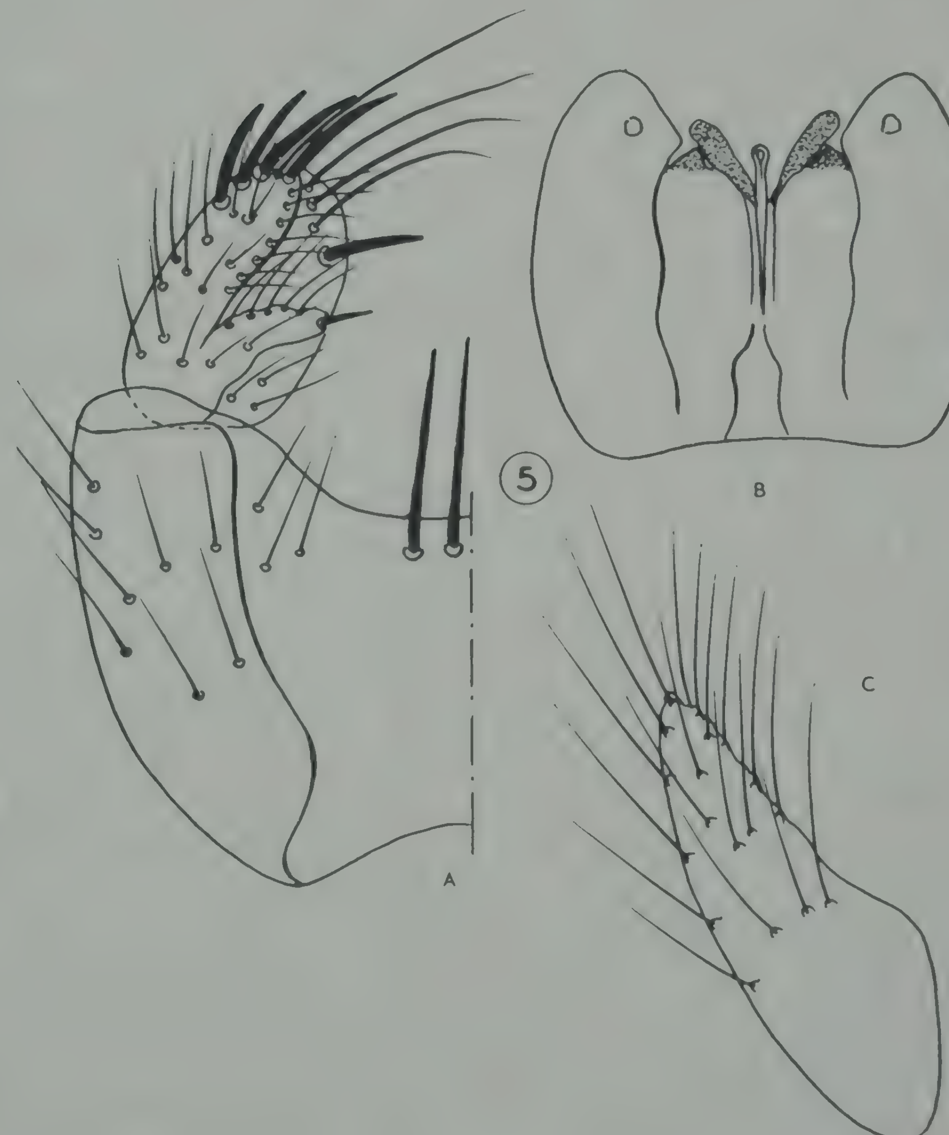
Note. This species is named in honor to its collector.

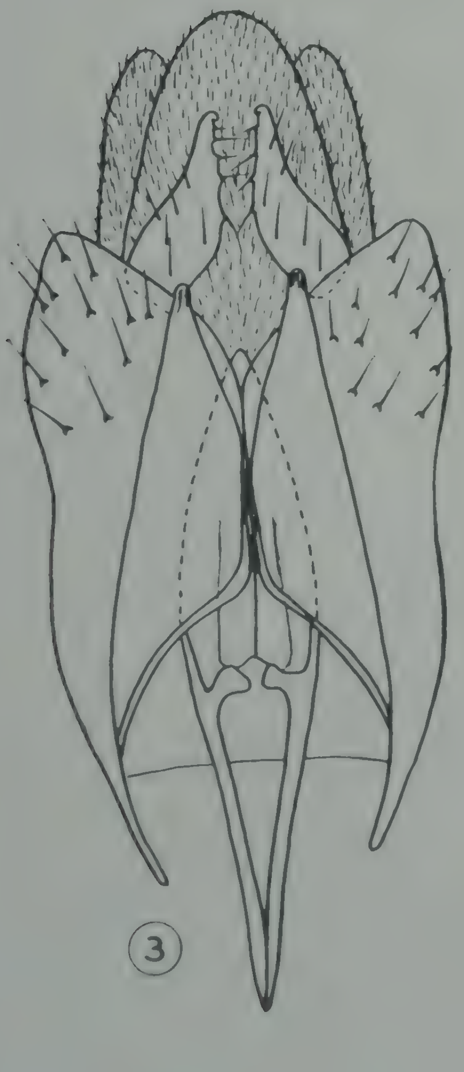


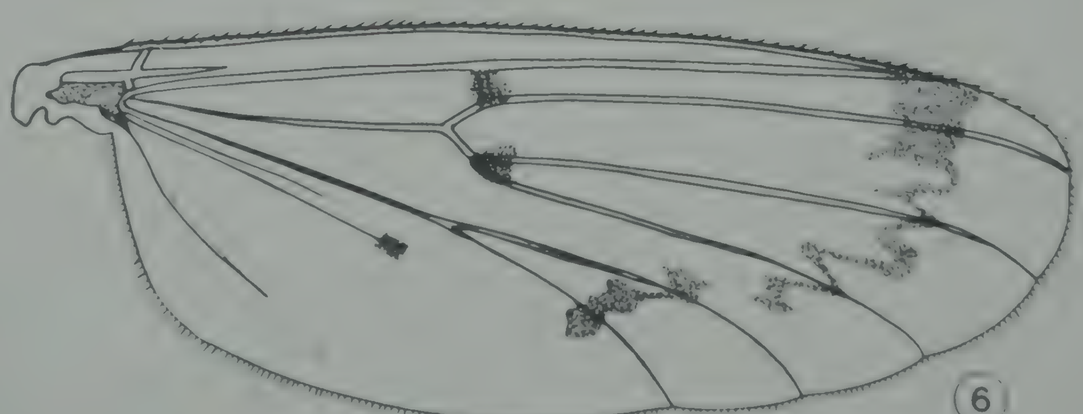












Figs. 1-5, 7. Male genitalia, dorso-ventral view. Fig. 6. Wing. 1, *Keroplatus* (*K.*) *golbachi* n. sp. 2, *K.* (*Cerotelion*) *dureti* n. sp. 3, *Platyura* (*Neoplatyura*) *aczéli* n. sp. 4, *Isoneuromyia tucumana* n. sp. 5A, 5B, 5C, *Epicypta* (*E.*) *aczéli* n. sp. 6, 7, *Mycetophila* (*M.*) *guanasi* n. sp.

Keroplatus (Neoceroplatus) minimax Edwards, 1934

1934. Edwards, Rev. Ent., 4: 358; 1941 Edwards, ibd., 12: 304; 1948 Lane, ibd., 19: 440.

Distribution. A single specimen. Prov. de Misiones, Deseado, 20. III. 1951 (J. P. Duret col.).

Keroplatus (Neoceroplatus) paicoenai Lane, 1950

1950. Lane, Dusenia, 1: 43.

We have two specimens. As the female has not been described we here select one of the female specimens as the allotype of this species.

Female. Abdomen broader and more flattened than in the male, markings more distinct. Cerci rounded and dark brown. Other characters as in the male.

Distribution. Allotype from Prov. Misiones, rio Paranaí, 13. III. 1951. Registered under n. 10.437 of our collections. A male from Prov. Misiones, Deseado, 1. XII. 1951 (J. P. Duret col.).

Subgenus Cerotelion

As we have found an additional new species, and as Freeman (1951) did not make a key for the species described by him, we have prepared a key to receive these additional Neotropical forms.

Key for Neotropical adults of *Cerotelion*

1. Haltere with whitish stem and blackish knob 2
   Haltere yellowish on both knob and stem 4

2. Wing with distinct dark markings; antenna short, the segments flattened and broader than long 3
   Wing evenly darkened but without distinct markings; antenna long, the segments longer than wide; head, thorax and legs blackish brown .... *nigricans* Lane, 1948

3. Mesonotum with three broad, brown stripes; darker species .... *funerea* Freeman, 1951
   Mesonotum with two stripes, lighter species .... *flavicornis* Freeman, 1951

4. Abdomen with narrow apical bands; scape and torus blackish or marked with black 5
   Abdomen with broad apical bands on all segments; scape and torus yellowish white; pleura dark brown but pteropleurite yellowish as well as margins of adjacent sclerites .... *dureti*, n. sp.

5. Mesonotum with five longitudinal lines; pleura, coxae and abdomen dark brown .... *enderleini* Lane, 1948
   Mesonotum yellow, with nude areas, so that only the blackish hairs form a pattern; pleura and coxae yellow .... *boracensis* Lane, 1950

Keroplatus (Cerotelion) funerea Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 19.

Distribution. Ter. Neuquen, Pucará, Parque Nacional Lanin, X. 1952 to III. 1953. (S. Shajovskoi col.).

Keroplatus (Cerotelion) enderleini Lane, 1948

1948. Lane, Rev. Ent., 19: 443.

Distribution. Prov. de Tucumán, Acheral, 15. XII. 1948 (J. P. Duret col.).

Keroplatus (Cerotelion) dureti n. sp.

Male. Mouth parts much reduced. Single palpal segment large and blackish. Face broad, yellowish. Antenna with yellowish white scape and torus; flagellar segments rounded, I yellowish at base and light brown, II to VII dark brown, the rest missing. Occiput dark brown, the ocellar callus slightly darker, three ocelli in a triangle and far from eye margin, the mesial one smaller.

Thorax: Pronotum yellow, with black hairs. Mesonotum yellowish with three blackish marks, sides also narrowly blackish; mesial mark elongate, triangular and from anterior portion up to prescutellar region but not reaching the scutellum; lateral marks from anterior fourth to scutellum, oblong and darker than the mesial one; covering of blackish hairs with nude areas. Scutellum yellowish brown, blackish at margin and with a row of many marginal setae. Postnotum brown, laterally yellowish, nude. Pleura with anepisternite and katepisternite blackish except the hind margin of katepisternite, nude, dull; pteropleurite yellow; pleurotergite dull blackish; hypopleurite yellowish.

Wing unicolorous. Haltere yellowish except base of knob which is slightly darker.

Legs: Front coxa yellow, the mid and hind ones light brown. Femora yellow. Tibiae and tarsi brown. Fore basitarsus slightly shorter than corresponding tibia.

Abdomen: Tergites dark brown with broad apical yellow bands over third or more of each segment and from I to VII; segment VII nearly completely yellow. Sternites I to V yellow, VI and VII blackish.

Genitalia: (Fig. 2). Basistyles with fused lobes at base, longer than broad. Dististyle longer than basistyle and ending in two incurved blunt, differentiated teeth. Other structures as in the figure.

Female. Unknown.

Type. Holotype male. To be returned to Dr. J. P. Duret, Buenos Aires. Argentina.

Type locality. Prov. de Buenos Aires, Cap. Federal, 27. IV. 1954 (J. P. Duret col.).

Note: This species is named in honor to its collector our friend Dr. J. P. Duret.

Platyura (Pyratula) paraguayana Edwards, 1934

1934. Edwards, Rev. Ent., 4 (3): 356.
1950. Lane, Dusenia, 1: 53.

When we mentioned this species it was wrongly ascribed to the subgenus *Pyrtaula*. We take this occasion to correct the mistake.

Distribution. Two females. Prov. Corrientes, Ituziango, IX. 1945 and Prov. de Misiones, Ramada Paso, IX. 1948 (J. P. Duret col.).

Platyura (Lyprauta) chacoensis Edwards, 1931

1931. Edwards, Konowia, 10: 77.
1939. Fisher, Trans. Ent. Soc. Am., 65: 228.
1940. Edwards, Rev. Ent., 11: 451.

Distribution. Prov. Salta, Aguaray, II. 1950 (R. Golbach col.), one specimen; Prov. Misiones, Corpus, IX. 1948, one specimen and Prov. Corrientes, B. de Astrada, IX. 1948 one specimen (J. P. Duret col.).

Note. This species has already been recorded from Argentina.

Platyura, (Lyprauta) nubilapex Edwards, 1940

1940. Edwards, Rev. Ent., 11: 452.

Distribution. Two specimens. Prov. Salta, Tartagal, II. 1950 (R. Golbach col.).

Platyura (Proceroplatus) terenoi Lane, 1950

1950. Lane, Dusenia, 1: 61.

Distribution. One specimen. Prov. de Tucumán, Tafí del Valle (2000 mts. alt.), 30. I. 1953 (P. Wygodzinsky col.).

Subgenus Neoplatyura

With the finding of a new species we have decided to key the species of our region.

Key for Neotropical adults of *Neoplatyura*

1. Vein M.3 not detached at base 2
Vein M.3 detached at base; abdomen dark brown, only the apex of segments with narrow bands; wing hyaline . . . . *saparai* Lane, 1950

2. Abdomen dark brown, when bands are present they are yellowish and narrow 3
Abdomen yellowish, tergites I, IV and V completely yellow, II and III with a broad apical blackish band, (in the female IV has also a very narrow apical blackish band); haltere yellowish but base of knob brownish; wing with a subapical diluted mark . . . . *aczéli*, n. sp.

3. Wing with a distinct subapical band; abdomen with base of tergites I, III and IV and sides of V yellowish . . . . *regularis* Edwards, 1934
Wing without such a band but smoky at apex; abdomen with very narrow bands on segments . . . . *ignobilis* Williston, 1896

Platyura (Neoplatyura) ignobilis Williston, 1896

1896. Williston, Trans. Ent. Soc. London, 257, fg. 9.
1909. Johannsen, Gen. Ins., 92: 23; 1909 Johannsen, Maine Agr. Exp. Sta. 172: 257.
1950. Lane, Dusenia, 1: 51.

Distribution. Prov. de Misiones, Los Halechos, III. 1954 (J. P. Duret col.).

Platyura (Neoplatyura) aczéli n. sp.

Male. Head: Mouth parts and palpus yellow. Frons yellow. Antenna with yellow scape and torus; flagellum blackish, short, slightly flattened. Occiput light brown, ocellar callus blackish, the three ocelli quite removed from the eye margin, mesial one smaller and inserted below laterals.

Thorax: Mesonotum brown with two dark elongate stripes from anterior margin to prescutellar area and two additional ones from anterior fourth to scutellum; covered with longish black hairs. Scutellum yellowish with a marginal row of setae. Pleura nude and yellowish including postnotum.

Wing hyaline with a small diluted spot over R. 4 and another band which is preapical and also diluted. Stem of M. weak, m-cu also weak at base. M. 3 not detached. M. 2 and M. 3 not reaching the wing margin. Haltere yellowish but the base of knob is light brown.

Legs: Coxae yellow. Femora yellow but the hind one is slightly darker basally. Tibiae and tarsi brown. Spurs 1-2-2, the inner one of T. II is very small.

Abdomen with tergites I, IV and V completely yellow, II and III with a broad apical blackish band, larger on II, the rest yellow; VI and VII blackish.

Genitalia (Fig. 3). Basistyles elongate, the lobes completely fused. Dististyle a small triangular structure as in figure. Mesosome elongate and with two ventral hooks. Other structures as in the figure.

Female. Mesonotal markings not so clear. Abdomen expanded and with segment IV also bearing a narrow blackish apical band. Cerci yellowish and rounded.

Types. Holotype male; allotype female; paratypes five males. Three paratypes registered in our collection under ns. 11.285 to 11.287. The remaining specimens to be returned to the Instituto Miguel Lillo, Tucumán and Dr. J. P. Duret, Buenos Aires, Argentina.

Type locality. Holotype from Prov. de Salta, Tonono, XII. 1949 (J. P. Duret col.); allotype from Embarcación, II. 1950; three paratypes from Embarcación II. 1950; one paratype from Tartagal, II. 1950 (R. Golbach col.) and one from Tartagal, XII. 1948 (J. P. Duret col.).

Note. This species is named in honor to our friend Dr. Martin L. Aczél from the Instituto Miguel Lillo, Tucumán, Argentina.

Platyura (Pyrtaula) alticola Lane, 1948

1948. Lane, Rev. Ent., 19: 450.

Seven females and ten males. This species appears to be common. We have noted quite a range of variation as to the mesonotal and abdominal markings so that some specimens are quite dark.

Distribution. Capital Federal, IX. 1948, V. 1947, I. 1954, IX. 1953; Prov. de Buenos Aires, G. Gonesa, IX. 1942, XI. 1942; Prov. de Chaco, Barranqueras, XI. 1949, Las Palmas, XI, 1949; Prov. de Cordoba, I. 1946; Prov. de Mendoza, Tupungato, II. 1952; Prov. de Misiones, IX. 1947; Prov. de Salta, Campo Quijano, XI. 1947 (J. P. Duret col.).

Isoneuromyia tucumana n. sp.

Male. Head: Mouth parts brown. Palpus with basal segments brown, the last one much elongated and blackish. Frons dark brown. Antenna with reddish dark brown scape and torus; flagellum blackish, somewhat flattened. Occiput black, the three ocelli removed from eye margin, the mesial one smaller; covered with blackish hairs.

Thorax: Pronotum blackish but posterior pronotum yellowish. Mesonotum black with white pruinosity and covered with longish black hairs leaving nude spaces. Scutellum black with many black margical setae. Postnotum black with white pruinosity. Pleura black but anterior spiracle yellow; hypopleurite brown.

Wing hyaline but about apical fourth darkened into a distinct mark; veins M.2 and M.3 not reaching the wing margin as well as the anal vein. Haltere with white stem and black knob.

Legs: Coxae yellow but with a brown mark at base of mid and hind ones. Femora yellow but blackish at apex. Tibiae and tarsi dark. Spurs 1-2-2, the outer ones shorter.

Abdomen dark brown with the following yellow markings: on tergites I and II with narrow basal bands, III and IV with broad basal bands, V completely yellowish, VI and VII blackish.

Genitalia: (Fig. 4). Basistyles fused at base, free at apex and quite long. Dististyle shorter than the basistyle, thickened at middle and ending in two strong, blackish teeth pointing inwards.

Female. Similar to male but with the following differences:—tergites I completely blackish, II to IV with broad, basal, yellowish bands while V to apex are yellowish. Cerci very long and slender, nearly as long as segment VII, whitish and constricted at apex to a point. Coxae as well as fore and mid femora blackish while hind femur is missing.

Types. Holotype male; allotype female; paratypes four males. Two paratypes to be retained and registered under ns. 11.288 and 11.289. Remaining specimens to be returned to the Instituto Miguel Lillo, Tucumán, Argentina.

Type locality. Prov. de Tucumán, Lacavera, VIII. 1953 (M. Aczél & R. Golbach col.), holotype; Tafí del Valle (2.000 mts. alt.), XII. 1950, allotype; Quebrada de la Toma (near Tafé Viejo), XII. 1950, paratypes (R. Golbach col.).

Note. Two of the paratypes have the first five tergites mostly yellow but conform otherwise with the descriptions. The definite apical wing mark at once separates this species from *I. argenteotomentosa* (Kertesz, 1909), which is the species with which it is more closely allied.

SUBFAMILY SCIOPHILINAE

All the specimens belonging to the tribe *Mycomyiini* were sent to Dr. E. I. Coher for determination.

Tribe Sciophilini

Sciophila cincticornis Edwards, 1940

1940. Edwards, Rev. Ent., 11: 458.

Distribution. One specimen from Prov. de Misiones, Iguazú Cué, XII. 1951 (J. P. Duret col.).

Leptomorphus neivai Edwards, 1940

1940. Edwards, Rev. Ent., 11: 452.

Distribution. One specimen from Prov. de Misiones, Cerro Azul, X. 1948 (J. P. Duret col.).

Megalopelma platyura Edwards, 1940

1940. Edwards, Rev. Ent., 11: 459.

Distribution. One specimen from Prov. de Tucumán, Lacavera, XI. 1951 (M. Aczél & R. Golbach col.).

Monoclona digitata Edwards, 1940

1940. Edwards, Rev. Ent., 11: 460.

Distribution. One specimen from PARAGUAY, Villarrica, VI. 1948 (Schade col.).

Monoclona maculata Edwards, 1933

1933. Edwards, Rev. Ent., 3: 307.

Distribution. One specimen from PARAGUAY, Villarrica, VI. 1948 (Schade col.).

Cluzobra binocellaris Edwards, 1934

1934. Edwards, Rev. Ent., 4: 362; 1940 Edwards, ibd., 11: 463.

Distribution. One specimen from Prov. de Chaco, Cierro Petizo, XI. 1947 (J. P. Duret col.).

Cluzobra fascipennis Edwards, 1940

1940. Edwards, Rev. Ent., 11: 464; 1948 Lane, Rev. Bras. Biol., 8: 254.

Distribution. One specimen from Prov. de Misiones, Los Helechos, V. 1949 (J. P. Duret col.).

Schnusea desanai Lane & Coher, 1950

1950. Lane & Coher, Rev. Bras. Biol., 10: 282.

Distribution. Four specimens from Prov. de Misiones, Deseado, XII. 1951 (J. P. Duret col.).

Schnusea sessilis Edwards, 1933

1933. Edwards, Rev. Ent., 3: 308.

DISTRIBUTION. One specimen from Prov. de Salta, Urundel, II. 1950 (R. Golbach col.).

TRIBE GNORISTINI

Dziedzickia hypsipile Lane, 1954

1954. Lane, Rev. Bras. Ent., 1: 101.

DISTRIBUTION. One specimen from Prov. de Misiones, Campo Ciera, X. 1948 (J. P. Duret col.).

Dziedzickia medea Lane, 1954

1954. Lane, Rev. Bras. Ent., 1: 103.

DISTRIBUTION. Three specimens from Prov. de Misiones, Aristobulo del Valle, II. 1951 (J. P. Duret col.).

TRIBE LEIINI

In our determinations, not all the specimens belonging to the genus *Leia* were studied. It is of interest to note the occurrence of *Procycloneura furcata* Freeman, 1951 in the Province of Tucumán, Argentina, as it extends considerably the range of this Chilean species.

Leia andirai Lane, 1950

1950. Lane, Rev. Bras. Biol., 10: 130.

Sixteen specimens. We noted variations as to the white markings on female antenna. While in five specimens the white is restricted to the last segment, on one of them only a portion of this segment is marked. In the male, the antenna is completely blackish. This species is close to *L. bilunula* Wiedemann, 1828, from which it can be separated by the abdominal markings.

DISTRIBUTION. Capital Federal, VIII. 1948, XI. 1950, VI. X. IX. 1949, III. IV. 1954, III. VII. 1952 (J. P. Duret col.).

Leia apinagei Lane, 1950

1950. Lane, Rev. Bras. Biol., 10: 152.

DISTRIBUTION. Two specimens Prov. de Misiones, Deseado, III. 1951 and Cerro Azul, V. 1949 (J. P. Duret col.).

Leia axillipunctum Enderlein, 1911

1911. Enderlein, Stet. Ent. Zeitg., 72: 198.

DISTRIBUTION. Two specimens Prov. de Misiones, Deseado, XII. 1950 (J. P. Duret col.).

Leia bilunula Wiedemann, 1828

1828. *Leia* Wiedemann, Aus. Zweifl. Ins., 1: 65.
1902. Kertesz, Cat. Dipt., 1: 83.
1909. Johannsen, Gen. Ins., 77.
1950. Shaw & Lane, Rev. Bras. Biol., 10: 255.

DISTRIBUTION. Three specimens from Capital Federal, XII. 1950 (J. P. Duret col.); Prov. de Tucumán, XII. 1950 (R. Golbach col.) and Lacavera, VI. 1950 (M. Aczél col.).

Leia bipartita (Arribálzaga, 1892)

1892. *Glaphyroptera* Arribalzaga, Bol. Ac. Nat. Sci. Cordoba, 12: 409.
1909. *Leia* Johannsen, Gen. Ins., 77.
1950. Shaw & Lane, Rev. Bras. Biol., 10: 254.

This species has been recorded from Argentina.

ADDITIONAL DISTRIBUTION. Capital Federal, IX. 1950 (J. P. Duret col.).

Leia diversipes Edwards, 1933

1933. Edwards, Rev. Ent., 3: 310.

DISTRIBUTION. One specimen from Prov. de Salta, S. Lorenzo, XI. 1947 (J. P. Duret col.).

Leia falculata Edwards, 1933

1933. Edwards, Rev. Ent., 3: 313.

DISTRIBUTION: One specimen from Prov. de Buenos Aires, Jose C. Paz, IX. 1939 (Oglobin col.).

Leia fasciata (Kertész, 1902)

1902. *Neoglaphyroptera* Kertész, Termes Fusz., 25: 574.
1931. *Leia* Edwards, Konowia, 10: 78.
1950. Shaw & Lane, Rev. Bras. Biol., 10: 255.

This species has been recorded from Argentina.

ADDITIONAL DISTRIBUTION. Fourteen specimens from Capital Federal, V. 1951 (J. P. Duret col.) and PARAGUAY, Villarrica, VI. 1945 (Schade col.).

Leia flavoscutellata (Arribálzaga, 1892)

1892. *Glaphyroptera* Arribalzaga, Bol. Ac. Nac. Córdoba, 12: 410.
1909. *Leia* Johannsen, Gen. Ins., 77.
1950. Shaw & Lane, Rev. Bras. Biol., 10: 254.

DISTRIBUTION. Thirteen specimens from Prov. de Buenos Aires, S. Nicolas, V. 1952; Prov. de Misiones, Pto. Rios, IX. 1948 (J. P. Duret col.) and PARAGUAY Villarrica, VI. 1945 (Schade col.).

Leia halterata (Kertész, 1902)

1902. *Neoglaphyroptera* Kertész, Term. Fuzet., 25: 575.
1909. *Leia* Johannsen, Gen. Ins., 78.
1950. Shaw & Lane, Rev. Bras. Biol., 10: 256.

DISTRIBUTION. Six specimens from Prov. de Misiones, Carbus, III. 1951 (J. P. Duret col.) and PARAGUAY, Villarrica, VII. 1949 (Schade col.).

Leia incompleta (Twinn & Curran, 1928)

1928. *Boletina* Twinn & Curran, Sci. Survey P. Rico & Virgin Isls., 11. syn. 1933 *Leia biamputata* Edwards, Rev. Ent., 3: 317.

Dr. Alan Stone wrote me the following in 19. II. 1954:—"I had occasion to determine a *Leia* from Puerto Rico and found that it agreed perfectly with specimens that you had determined as *Leia biamputata* Edwards, 1933. I also noted that there seemed no way of distinguishing the specimen from what Curran described as *Boletina incompleta* in 1928. It would seem, therefore, that *Leia biamputata* is a synonym of *L. incompleta* (Curran)."

As Edwards (1933, Rev. Ent., 3 (3): 314) described a species as *Leia incompleta* Edward's name becomes an homonym and we here propose the name of *Leia stonei n. n.* for this species.

DISTRIBUTION. Thirty specimens from Prov. de Salta, Embarcación, Aguaray, Tartagal, Urundel, II. 1950 and Prov. de Tucumán, Aconquija, XII. 1950 and Lacavera, XI. 1950 (R. Golbach col.).

Leia monoleuca Edwards, 1933

1933. Edwards, Rev. Ent., 3: 312.

DISTRIBUTION. One specimen from Prov. de Misiones, Iguazú, X. 1948 (J. P. Duret col.)

Leia paranensis Edwards, 1933

1933. Edwards, Rev. Ent., 3: 313.

DISTRIBUTION. Twelve specimens from Prov. de Misiones, Deseado. III. 1949, XI. 1954, Aristobulo del Valle, II. 1951, B. de Irigoyen, III. 1951 (J. P. Duret col.).

Leia picticornis (Kertész, 1902)

1902. *Neoglaphyroptera* Kertész, Term, Fuzet, 25: 578.
1909. *Leia* Johannsen, Gen. Ins., 79.

DISTRIBUTION. Five specimens from Prov. de Misiones, Deseado, III. IX. XII. 1951 (J. P. Duret col.).

Leiella ochreocalcar Enderlein, 1911

1911. Enderlein, Stet. Ent. Zeitg., 72: 200.
1933. Edwards, Rev. Ent., 3: 320.

DISTRIBUTION. Five specimens from Prov. de Chaco, Berquilla, XI. 1949 (J. P. Duret col.); Prov. de Salta, Embarcación, II. 1950 (R. Golbach col.), San Lorenzo I. 1949 (M. Aczél col.); Prov. de Tucumán, Quebrada la Toma, XII. 1950 (R. Golbach col.).

Leiella zonalis Edwards, 1931

1931. Edwards, An. & Mag. N.H., 10: 259; 1952 Lane, Rev. Ent., 3: 139.

A series of eighteen species which show the yellowish white of tergites III and IV extensively distributed, more so in two of the males.

Distribution. Prov. de Santa Fé, Vera, XII. 1950; Prov. de Chaco, Laguna Limpia, XII. 1949, Capitan Solari, XI. 1949, Est. Girasol, XII. 1949 (J. P. Duret col.), Col. Benitez, XII. 1948 (R. Golbach col.); Prov. de Tucumán, Lacavera, XI. 1951 (R. Golbach col.).

Paraleia nubilipennis (Walker, 1836)

1836. *Leia* Walker, Trans. Lin. Soc. London, 17: 334.
1892. Arribálzaga, Bol. Ac. Nac. Cordoba, 12: 408.
1909. Johannsen, Gen. Ins., 93: 79.
1913. *Acrodicrania* Edwards, An. & Mag. N.H., 12: 55.
1946. Stuardo, Cat. Dipt. Chile, 58.
1951. *Paraleia* Freeman, Dipt. Pat. & S. Chile, 3: 74, 75.

Distribution. Twenty-two specimens from Terr. Santa Cruz, Lago Argentino, II. 1950 (P. Willink col.) and CHILE, Magallanes, El Ganso, II. 1953 (R. Rodriguez col.).

Megophthalmidia divergens Edwards, 1932

1932. Edwards, Rev. Ent., 2: 141.

Distribution. One specimen from Prov. de Tucumán, Quebrada La Toma, XII. 1950. (R. Golbach col.).

Procycloneura paranensis Edwards, 1932

1932. Edwards, Rev. Ent., 2: 141.

Distribution. One specimen from Prov. de Misiones, Aristobulo del Valle, II. 1951 (J. P. Duret col.).

Procycloneura furcata Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 80.

Distribution. Prov. de Tucumán, Lacavera, XI. 1951 (Aczél & Golbach col.); Quebrada la Toma, XI. 1950 (R. Golbach col.).

Tetragoneura borgmeieri Edwards, 1932

1932. Edwards, Rev. Ent., 2: 142; 1952 Lane, ibd., 14: 408.

Distribution. One specimen from Prov. Corrientes, S. Benito, IV. 1950 (J. P. Duret col.).

Tetragoneura galea Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 84.

Distribution. One specimen from Ter. Neuquen, Villa Angostura (S. Shajovskoi col.).

Tetragoneura sinuata Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 83.

Distribution. One specimen from Ter. Neuquen, Pucará, Parque Nacional Lanin, XI. 1952 to II. 1953 (S. Shajovskoi col.).

SUBFAMILY MYCETOPHILINAE

This subfamily was the one which was best represented in the collections and from a zoogeographical point of view, the most interesting. The following species from the Chilean center of dispersal and endemism were found to extend their range into Argentinian provinces not belonging to it:—*Trichonta fasciata* Freeman, 1951; *Mycetophila pectinata* Freeman, 1951, and *Mycetophila triordinata* Freeman, 1953.

On the other hand, the genus *Epicypta* has continued to be negative to the Chilean center.

Zygomyia freemani Lane, 1951

1951. Lane, Dusenia, 2: 248.

We hesitated in the determination of this material as the specimens had different mesonotal markings. Besides a stronger tinge, the marks spread to the sides and the mesial one is divided.

When a larger series is examined, there is the possibility that this may prove a distinct subspecies.

DISTRIBUTION. Three specimens. Prov. de Salta, Urundel, III. 1950 (R. Golbach col.).

Zygomyia ornatipennis Lane, 1948

1948. Lane, Rev. Ent., 19: 241; 1951 Lane, Dusenia, 2 (4): 250.

DISTRIBUTION. One specimen. Prov. de Misiones, Aristobulo del Valle, 28. III. 1954 (J. P. Duret col.).

Cordyla brevicornis (Enderlein, 1911)

1911. *Allodia* Enderlein, Stet. Ent. Zeitg., 72: 204.
1941. *Neallodia* Edwards, Rev. Ent., 12: 311.
syn. 1932. *Neallodia flavida* Edwards, Rev. Ent., 2: 146.
1947. *Trichonta brasiliana* Lane, Rev. Ent., 18: 448.

Dr. Paul Freeman of the British Museum (Natural History) suggested that our *Trichonta brasiliana* could be synonymous with this species. A comparison of our material with a specimen determined by Edwards as *brevicornis* has shown that they are conspecific and for this reason we here synonymize our species.

The number of hairs on the anepisternite and the production of the costal vein is variable in the large series of specimens which we have examined. For this reason we also consider *N. flavida* Edwards, 1932, a synonym of *C. brevicornis* (Enderlein, 1911).

DISTRIBUTION. Twelve specimens. Prov. de Salta, Tartagal, II. 1950; Aguaray, II. 1950; Urundel, II. 1950; Embarcación, II. 1950 (R. Golbach col.); one specimen from PARAGUAY, Villaraica, VI. 1945 (Schade col.).

Trichonta fasciata Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 97.

DISTRIBUTION. Five specimens. Prov. de Tucumán, Lacavera, XII. 1951 (M. Aczél col.).

Epicypta (Epicypta) aczéli n. sp.

MALE. Head: Mouth parts and palpus yellowish. Antenna with scape, torus and first four or five segments yellowish, the rest darkened. Occiput brown in the center and lighter on the sides.

Thorax: Mesonotum yellow with a very large black, rounded mark over posterior two thirds but not invading margins and fused with the two prescutellar blackish spots; covered with decumbent yellowish hairs. Scutellum yellowish but sides and margins brownish black. Postnotum blackish in the center and yellowish on the sides. Pleura yellowish; anepisternite brown anteriorly and bearing golden hairs on posterior portions; pteropleurite and pleurotergite brown.

Wing hyaline. Posterior fork slightly beyond anterior one. Haltere yellow.

Legs: Coxae, trochanteres and femora, yellowish; hind femur narrowly blackish at apex. Tibiae yellowish, hind one darkened at base. Mid tibia with 5 d., 3 e., 2 v. and 1 i. setae. Hind tibia with 6 d., 3 subdorsal and 3 i. setae.

Abdomen blackish except middle of base and apex of segments II to V and apex of VI which are yellowish.

Genitalia: (Fig. 5). Basistyle with lobes fused, two stout internal setae present. Dististyle rounded and with four, stout and differentiated setae on its apical margin and another on the inner portion above middle and at right angles; a protuberance ending in a short stout seta is also present. Mesosome as in figure. Ninth tergite as high as dististyle.

FEMALE. Similar to male but abdomen with much narrower markings. Cerci small, elongate and yellowish.

TYPES. Holotype male; allotype female; paratypes seventeen males and females. Holotype, allotype and five paratypes to be returned to the Instituto Miguel Lillo, Tucumán, Argentina; one paratype to be sent to the British Museum (Natural History); one paratype to be sent to the U.S. National Museum, Washington, D.C.; four paratypes to be returned to Dr. J. P. Duret, Buenos Aires, Argentina and the remaining paratypes registered in our collections under ns. 10.393 to 10.399.

Type locality. Prov. de Salta, Embarcación, II. 1950 (holotype), Aguaray, I. 1950 (allotype); Tartagal, II. 1950 (five paratypes), Urundel, II. 1950 (oneparatype), Que brada La Toma, XII. 1950 (one paratype); Prov. de Tucumán, Aunguigea, XII. 1950 (one paratype), (all collected by R. Golbach); Prov. de Corrientes, Col. Pellegrini, III. 1951 (four paratypes); Prov. de Chaco, Cierro Petizo, XI. 1949 (J. P. Duret col.). BRASIL, State of Goiáz, Corumbá, XI. 1945 (M. P. Barretto col.); State of S. Paulo, Ribeirão Preto, rio Tamanduá, X. 1954 (J. P. Duret et M. P. Barretto col.) two paratypes; TRINIDAD (B.W.I.), Monte Serrat, VI. 1913 (A. Busck col.), one paratype.

Note. We take pleasure in naming this species in honor to our friend Dr. Martin L. Aczél of the Instituto Miguel Lillo, Tucumán, Argentina, who has done excellent work on many groups of Neotropical Diptera.

This species differs from *E. goianensis* and *E. brasiliensis* because of the scutellar markings; from *E. maupiensis* because it has no longitudinal dark scutellar stripe. From all species of its group because the posterior black mesonotal marks covers the whole posterior portion of disk but does not extend to the sides. On the other hand the male genitalia is quite distinct from all species hitherto described in this subgenus.

Epicypta (*Epicypta*) *brasiliana* Edwards, 1932

1932. *Delopsis* Edwards, Rev. Ent., 2: 147; 1947 Lane, ibd., 18: 454.
1951. *Epicypta* Lane, Dusenia, 2: 338.

Distribution. One specimen. Prov. de Salta, Aguaray, II. 1950 (R. Golbach col.).

Epicypta (*Epicypta*) *brasiliensis* (Enderlein, 1911)

1911. *Mycetophila* Enderlein, Stet. Ent. Zeitg., 72: 171.
1947. *Delopsis* Lane, Rev. Ent., 18: 455; 1951 *Epicypta* Lane, Dusenia, 2: 340.

Distribution. One specimen. Prov. de Salta, Aguaray, II. 1950 (R. Golbach col.).

Epicypta (*Epicypta*) *duanasi* Lane, 1951

1951. Lane, Dusenia, 2: 377.

Distribution. Five specimens. Prov. de Salta, Tartagal, Aguaray and Urundel, II. 1950 (R. Golbach col.).

Epicypta (*Epicypta*) *goianensis* (Lane, 1947)

1947. *Delopsis* Lane, Rev. Ent., 18: 456.

Distribution. One specimen. Prov. de Misiones, Cerro Azul, 3. V. 1949 (J. P. Duret col.).

Epicypta (*Epicypta*) *maculipennis* (Enderlein, 1911)

1911. *Plastacephala* Enderlein, Stet. Ent. Zeitg., 72: 178.
1948. *Delopsis* Lane, Rev. Ent., 19: 277.

Distribution. One specimen. Prov. de Salta, Tartagal, II. 1950 (R. Golbach col.).

Epicypta (*Epicypta*) *planiventris* (Enderlein, 1911)

1911. *Plastacephala* Enderlein, Stet. Ent. Zeitg., 72: 176.
1939. *Delopsis* Fisher, Trans. Ent. Soc. Am., 65: 236.
1941. Edwards, Rev. Ent., 12: 311.
1951. *Epicypta* Lane, Dusenia, 2 (5): 336.

Distribution. One specimen. Prov. de Misiones, El Salto Encantado, 19. X. 1948 (J. P. Duret col.).

Epicypta (*Boscmyia*) *lenguasi* Lane, 1954

1954. Lane, Rev. Bras. Ent., 2: 121.

Distribution. One specimen. Prov. de Misiones, Bemberg, XI. 1948 (J. P. Duret col.).

Epicypta (*Callicypta*) *inornata* Lane, 1948

948. *Epicypta* Lane, Rev. Ent., 19: 237.
954. *Epicypta* (*Callicypta*) Lane, Rev. Bras. Ent., 2:134.

Distribution. Three specimens. Prov. de Tucumán, Quebrada la Toma, XII. 1950; rov. de Salta, Tartagal, II. 1950 (R. Golbach col.).

Mycetophila (Mycetophila) amplipennis Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 115.

Distribution. A single specimen. Terr. de Neuquen, Pucara, XI. 1952 (Schajovskoi col.).

Mycetophila (Mycetophila) banhumai Lane, 1952

1952. Lane, Dusenia, 3 (6): 424.

Distribution. Eleven specimens. Prov. de Tucumán, Tafí del Valle, VII. 1947, XII. 1947 (R. Golbach col.).

Mycetophila (Mycetophila) curiaensis Lane, 1952

1952. Lane, Dusenia, 3: 425.

Distribution. Three specimens. Prov. de Salta, Aguaray, II. 1952; Prov. de Tucumán, Tafí del Valle, VII. 1947 (R. Golbach col.).

Mycetophila (Mycetophila) freemani Lane, 1948

1948. Lane, Rev. Ent., 19: 256.

Distribution. Two specimens. Prov. de Tucumán, Lacavera, XII. 1951 (M. Aczél & R. Golbach col.).

Mycetophila (Mycetophila) guanasi n. sp.

Male. Head and mouth parts yellow. Palpus yellow but segment I brownish on one side, the segments long, last one the longest. Antenna with yellow scape and torus; flagellar segment I with a brown basal ring, the rest yellow, other segments with a dilute apical brownish ring which becomes larger and distinct on apical ones, the rest yellow.

Thorax: Mesonotum yellow on the sides, brownish in the middle, with two prescutellar brown spots and also brown spots over the root of wing. Scutellum yellow with large brown markings; four scutellar setae. Postnotum brown, laterally with whitish pruinose marks. Pleura; anepisternite brown, yellow mesially and below up to katepisternite, with golden hairs as well as five stout setae; katepisternite yellow but anteriorly and below with a brown mark; pteropleurite brown above, yellow below, with six setae in a row; pleurotergite brown with many posterior setae; hypopleurite yellow, below and behind with a brown mark and two setae besides three or four small ones.

Wing with veins and markings as in Fig. 6. Haltere yellowish.

Legs: Coxae yellow, extreme apex with brown markings. Femora yellow but with brown marks at base and apex. Tibiae yellow but with a broad apical brown band. Mid tibia with 5 d., 4 e., o v. and 8 i. setae (hind femora, tibiae and tarsi missing).

Abdomen yellowish. Tergite I broadly brown in the middle where there are some stout setae.

Genitalia. (Fig. 7). Basistyle with lobes fused and hollowed out so as to receive the dististyles, the upper margin sinuate as in the figure. Mesosome not seen. Ninth tergite finger shaped.

Female. Unknown.

Type. Holotype male, to be returned to the Institute Miguel Lillo, Tucumán, Argentina.

Type locality. Prov. de Tucumán, Tafí del Valle (2.000 mts. alt.), 12. XII. 1950 (R. Golbach col.).

Note. This species is near *M. armatura* Freeman, 1951, from which it can be readily separated by the wing markings and male genitalic structures.

Mycetophila (Mycetophila) guaraiasi Lane, 1952

1952. Lane, Dusenia, 3 (6): 427.

Distribution. Four specimens. Prov. de Misiones, B. de Irigoyen, III. 1954 (J. P. Duret col.); Prov. de Salta, Aguaray, II. 1950 (R. Golbach col.).

Mycetophila (Mycetophila) iheringi Lane, 1948

1948. Lane, Rev. Ent., 19: 260; 1952 Lane, Dusenia, 3 (6): 433.

Distribution. One specimen. Prov. de Misiones, Alba Pose, X. 1949 (J. P. Duret col.).

Mycetophila (*Mycetophila*) *illita* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 122.

Distribution. One specimen. CHILE, Magallanes, El Ganso, III. 1953 (R. Rodriguez col.).

Mycetophila (*Mycetophila*) *nervitacta* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 116.

Distribution. Two specimens. Terr. de Santa Cruz. Lago Argentino, II. 1953 (Willink col.).

Mycetophila (*Mycetophila*) *picea* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 119.

Distribution. Five specimens. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (*Mycetophila*) *theresae* Edwards, 1932

1932. Edwards, Rev. Ent., 2: 148: 1948 Lane, ibd., 19: 255.

Distribution. Four specimens. Prov. de Tucumán, Tafí del Valle, XI. 1947 (R. Golbach col.).

Mycetophila (*Mycetophila*) *triangulifera* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 110.

Distribution. Five specimens. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (*Oromyceta*) *wygodzinskyi* (Lane, 1947)

1947. *Delopsis* Lane, Rev. Ent., 18: 456.

Distribution. One specimen. Prov. de Salta, Aguaray, II. 1950 (R. Golbach col.).

Mycetophila (*Abmyceta*) *acarisi* n. sp.

Male. Head: Mouth parts and palpus yellowish brown. Clypeus brown. Antenna with yellowish scape and torus; flagellum with basal segment yellowish, the other segments brown. Occiput brown.

Thorax: Mesonotum yellowish with three brown longitudinal stripes. Scutellum yellow in the middle-brownish on the sides, with four marginal setae. Postnotum yellowish. Pleura brownish with lighter portions. Three anepimeral; two pteropleural and two or three pleurotergal setae; hypopleurite yellowish, with one or two very small posterior hairs.

Wing with veins and markings as in Fig. 8. Haltere yellowish.

Legs: Coxae yellowish. Femora yellow, apices narrowly darker. Tibiae yellowish. Mid tibia with 4 d., 1 e., 1 v. and ⅔ i. setae. Hind tibia with 6 d. and 7 e.

Abdomen blackish with narrow apical bands.

Genitalia: (Fig. 9). Basistyle with the lobes fused, quadrate. Dististyle with lobes as in Fig. 9. Ninth tergite elongate, with a preapical notch and as in Fig. 9.

Female. Similar to the male. Cerci elongate and dark brown.

Types. Holotype male; allotype female; paratypes three females. Holotype, allotype and one paratype to be returned to the Instituto Miguel Lillo, Tucumán. Two paratypes registered under ns. 11.397 and 11.398.

Type locality. Prov. de Tucumán, Tafí del Valle, 6-12, XII. 1950 (R. Colbach col.).

Note. This species is near *M. sinuata* Freeman, 1951 from which it can be separated by the wing markings and male genitalic structures.

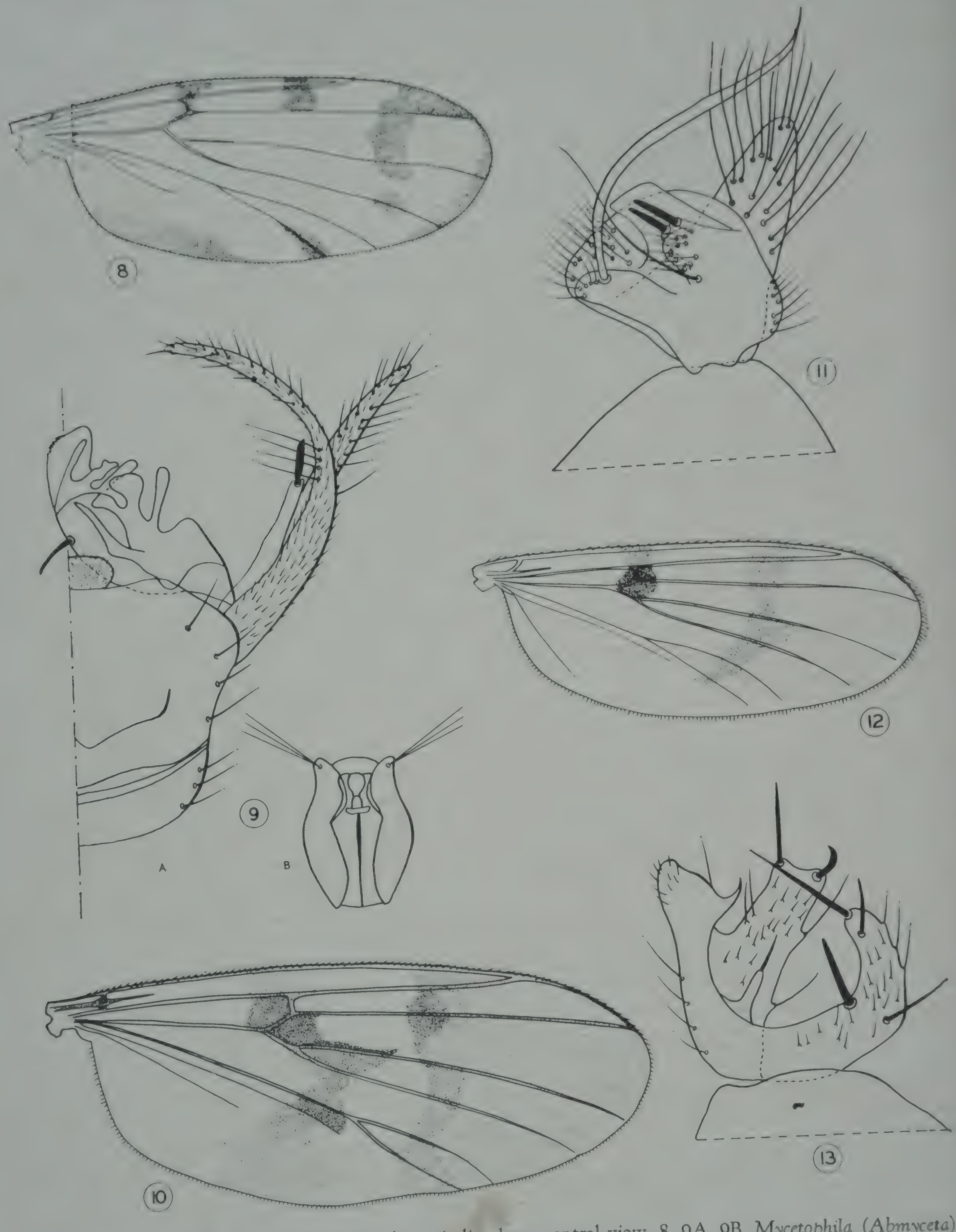
Mycetophila (*Abmyceta*) *argentina* n. sp.

Male. Head and palpus blackish. Antenna with brown scape and torus; flagellum with segment I yellow at base, the rest blackish as well as other segments.

Thorax: Mesonotum blackish, humeral region yellowish as well as very narrow portions of prescutellar region and above root of wing. Scutellum blackish but margins broadly yellowish; four marginal setae. Pleura blackish; hypopleurite brownish.

Wing with veins and markings as in Fig. 10. Haltere yellow.

Legs: Coxae yellowish with diluted brown markings. Femora yellowish, the dorsum and venter with indefinite brown markings. Tibiae yellowish, apex of mid and hind ones



Figs. 8, 10, 12. Wing. Figs. 9, 11, 13. Male genitalia, dorso-ventral view. 8, 9A, 9B, *Mycetophila* (*Abmyceta*) *acarisi* n. sp. 10, 11, *M.* (*A.*) *argentina* n. sp. 12, 13, *M.* (*A.*) *golbachi* n. sp.

darker. Mid tibia with 4 d., 2 e., 2 v., and 8 i. setae in a row, Hind tibia with 6 d. and 6 e. setae.

Abdomen blackish.

Genitalia: (Fig. 11). Basistyles united and quadrate. Dististyle as in the figure. Mesosome ovate, the upper portions surpassing the lateral flaps and rounded; the lateral flaps pointed. Ninth tergite subtriangular and shorter than the height of basistyle.

Female. Similar to male. Cerci brown and elongate.

Types. Holotype male; allotype female; paratypes three males and three females. Holotype, allotype and three paratypes returned to the Instituto Miguel Lillo, Tucumán, Argentina. Three paratypes registered in our collection under ns. 10.409 to 10.411.

Type locality. Prov. de Santa Cruz, Lago Argentino, 26. II. 1953 (Dr. W. Willink col.).

Mycetophila (*Abmyceta*) *borgmeieri* Edwards, 1932

1932. Edwards, Rev. Ent., 2: 149: 1948 Lane, ibd., 19: 258.

Distribution. Twenty specimens. Prov. de Tucumán, Tafí del Valle, XII. 1947 (R. Golbach col.).

Mycetophila (*Abmyceta*) *canicula* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 127.

Distribution. Ten specimens. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (*Abmyceta*) *clavigera* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 125.

Distribution. Hundreds of specimens from Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Note. The above mentioned material shows a wide range of variation and the probability that it represents a complex group of similar species must be taken in consideration.

Mycetophila (*Abmyceta*) *constricta* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 128.

Distribution. Two specimens. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (*Abmyceta*) *demacuri* Lane, 1951

1951. Lane, Trans. R. Ent. Soc. London, 106:405.

Distribution. Five specimens. Prov. de Tucumán, Quebrada La Toma, XII. 1951 (M. Aczél & R. Golbach col.); Prov. de Salta, Aguaray, II. 1950 (R. Golbach col.).

Mycetophila (*Abmyceta*) *dichaeta* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 126.

Distribution. Two specimens. Prov. de Tucumán, Tafí del Valle, VII. 1947 and XII. 1950 (R. Golbach col.).

Mycetophila (*Abmyceta*) *flavolunata* Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 122.

Distribution. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (*Abmyceta*) *golbachi* n. sp.

Male. Head brownish yellow. Palpus yellowish. Antenna with scape, torus and first three or four segments yellowish, the rest darkened.

Thorax: Mesonotum brown; covered with brown hairs and dark setae. Scutellum brown but darker than mesonotum. Pleura with anterior spiracular sclerite, upper portion of pronotum and basal portion of pteropleurite yellowish, the rest dark brown.

Wing with markings and veins as in Fig. 12. Haltere yellow.

Legs: Coxae yellow. Trochanteres brown. Femora yellow, mid and hind ones dorsally darkened as well as narrowly at apex. Tibiae yellowish, mid and hind ones darker apically. Mid tibia with 5 d., 3 e., 1+2 v. and a row of 6-7 i. setae. Hind tibia with 5 d. and 7e. setae.

Abdomen blackish.

Genitalia: (Fig. 13). Basistyles with the fused lobes broader than high. Dististyle as in figure. Mesosome with lateral upper flaps high and pointed, the mid portion rounded. Ninth tergite shorter than basistyle and subtriangular.

Female. Similar to male. Cerci elongate, slender and yellowish.

Types. Holotype male; allotype female; paratypes six males and three females. Holotype, allotype and four paratypes returned to the Instituto Miguel Lillo, Tucumán, Argentina; five paratypes registered in our collection under ns. 10.413 to 10.417.

Type locality. Prov. de Tucumán, Tafí del Valle, XII. 1950 (R. Golbach col.), one paratype from La Cavera, VI. 1951 (M. Aczél et R. Golbach col.).

Note. We take pleasure in naming this species in honor to Dr. R. Golbach who collected a large portion of the material here studied.

By the wing markings this species would be placed near *M. comifera* and *M. clavigera* but, besides the outer mark of wing being (in *M.golbachi*) as a slender stripe, the male genitalia is quite different.

Mycetophila (*Abmyceta*) *tapuiai* n. sp.

Male. Head: Mouth parts and palpus yellowish brown. Antenna with scape, torus and base of flagellar segment I yellowish, the rest dark brown. Occiput brown.

Thorax: Mesonotum yellowish, with three indistinct brown longitudinal marks. Scutellum brownish, with four marginal setae. Postnotum brownish. Pleura dark brown but yellowish in the middle; anepisternite with three stout setae; pteropleurite with two or three stout setae; pleurotergite with a few setae.

Wing with a dark spot which from r-m reaches base of upper fork; a second dark spot at apex of wing and slightly below R. 4. Second fork of vein very much beyond the first so that its stem is about three times the length of respective fork. Haltere yellowish.

Legs: Coxae yellow, last one slightly darker at apex. Femora yellow, the last one slightly darker at base and apex. Tibiae yellowish. Mid tibia with 4 d., and 2 v. setae. Hind tibia with 5 d. and 7 e. setae.

Genitalia: (Fig. 14). Greatly enlarged, nearly as large as thorax. Basistyles fused, inflated forming a rounded structure, at apex a row of differentiated setae on each side. Dististyle invaginated on the basistyles, the lobes complex and as in the figure. Ninth tergites united at base and forming two slender filaments.

Female. Unknown.

Types. Holotype male; paratype one male. Holotype to be returned to the Instituto Miguel Lillo, Tucumán, Argentina; the paratype registered in our collection under n. 11.399.

Type locality. Prov. de Tucumán, Lacavera, XII. 1951 (Aczél et Golbach col.), holotype; Quebrada de Cainzo (near Tafi Viejo), 8. XI. 1950 (R. Golbach col.), paratype.

Note. This species is near *M. guatensis* but the lower fork is much beyond the upper one and the male genitalic structures are completely different from those of the subgenus.

Mycetophila (*Abmyceta*) *tucumana* n. sp.

Male. Head blackish brown. Palpus yellow. Antenna with scape and torus brownish; flagellum with basal segments blackish but base yellow, the rest darkened.

Thorax: Mesonotum yellowish with three brown marks which are fused and indistinct; covered with yellowish hairs and brown setae. Scutellum brown with four marginal setae. Pleura brown.

Wing hyaline with two spots, the veins and markings as in Fig. 15. Haltere yellow.

Legs: Coxae yellow. Femora yellow, mid and hind ones darkened dorsally and at apex. Tibiae yellow, mid and hind ones darkened at apex. Mid tibia with 5 d., 3 e., 2+1 v. and 1 i. setae. Hind tibia with 5 d. and 6 e. setae.

Abdomen blackish.

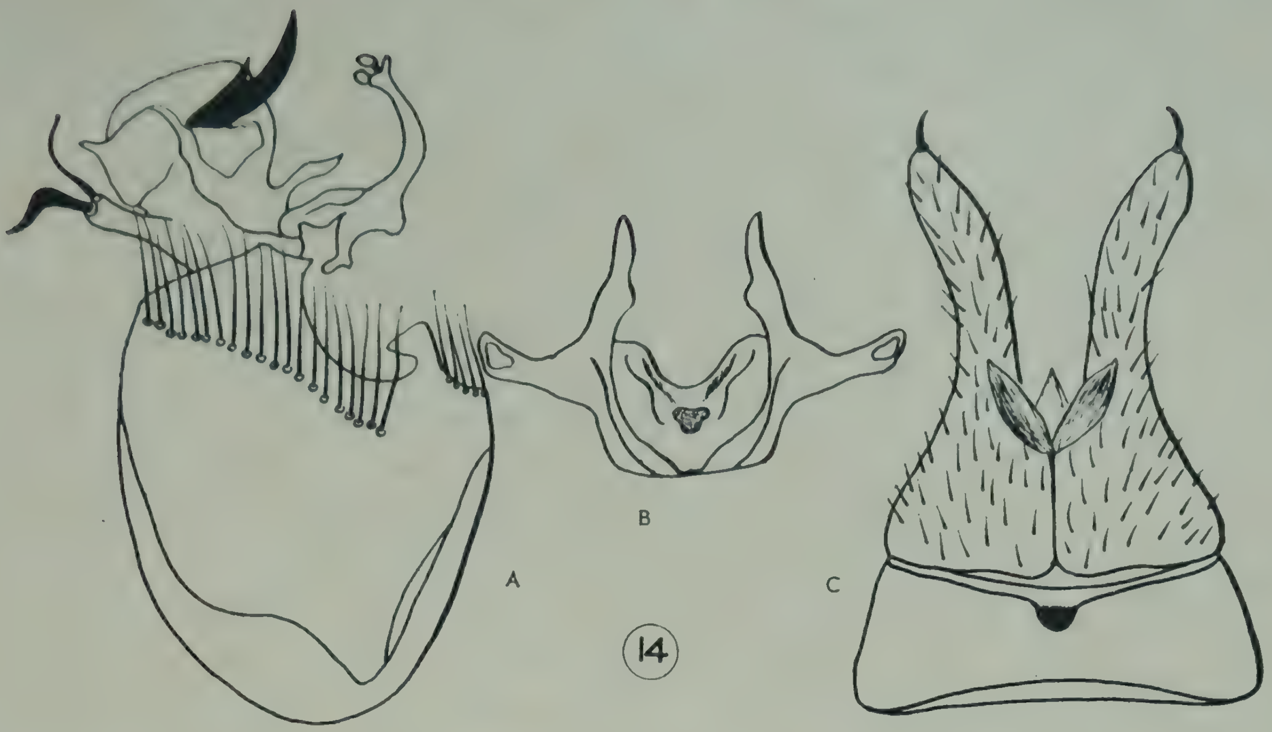
Genitalia: (Fig. 16). Basistyle with lobes fused and quite broader than long, shallow in the middle. Dististyle as in Fig. 16. Mesosome with upper portions quite expanded. Ninth tergite with lobes as high as basistyle.

Female. Similar to male. Cerci small and rounded.

Types. Holotype male; allotype female; paratypes three males and six females. Holotype, allotype and four paratypes returned to the Instituto Miguel Lillo, Tucumán, Argentina. Five paratypes registered in our collection under ns. 10.404 to 10.408.

Type locality. Prov. de Tucumán, Tafí del Valle, 12 XII. 1947; Quebrada La Toma, 21. XI. 1950, one paratype (R. Golbach col.); La Cavera (M. Aczél et R. Golbach col.), one paratype.

Note. This species is, as to adult markings, similar to *M. flabellifera* from which it can be separated by the chaetotaxy of mid tibiae. On the other hand the male genitalia is different from all other species belonging to this subgenus.



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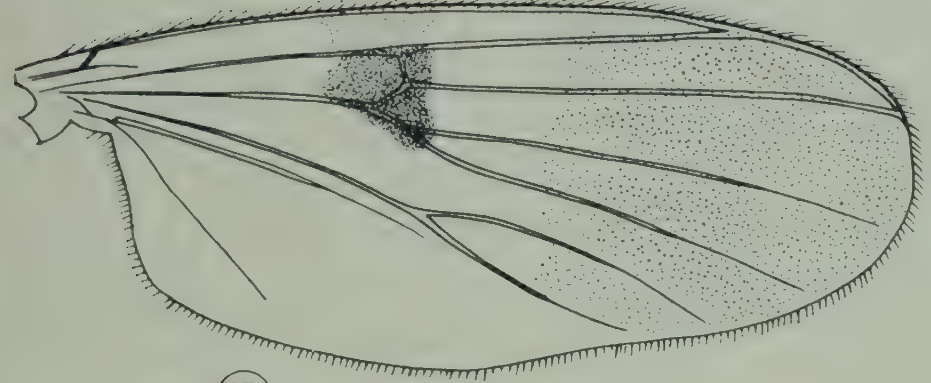

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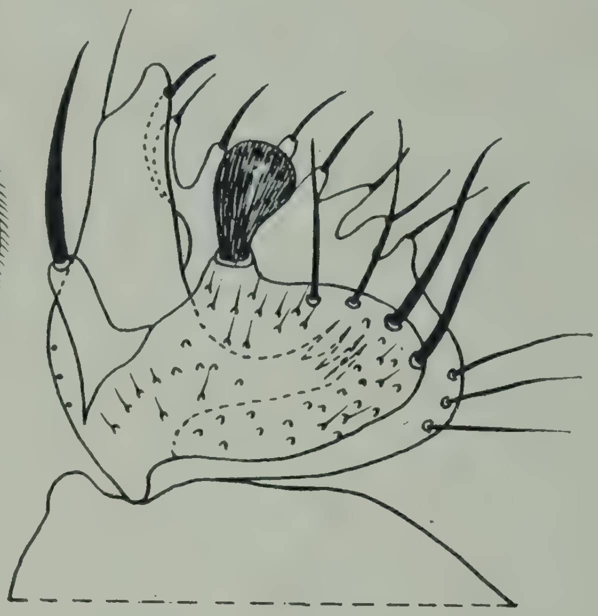

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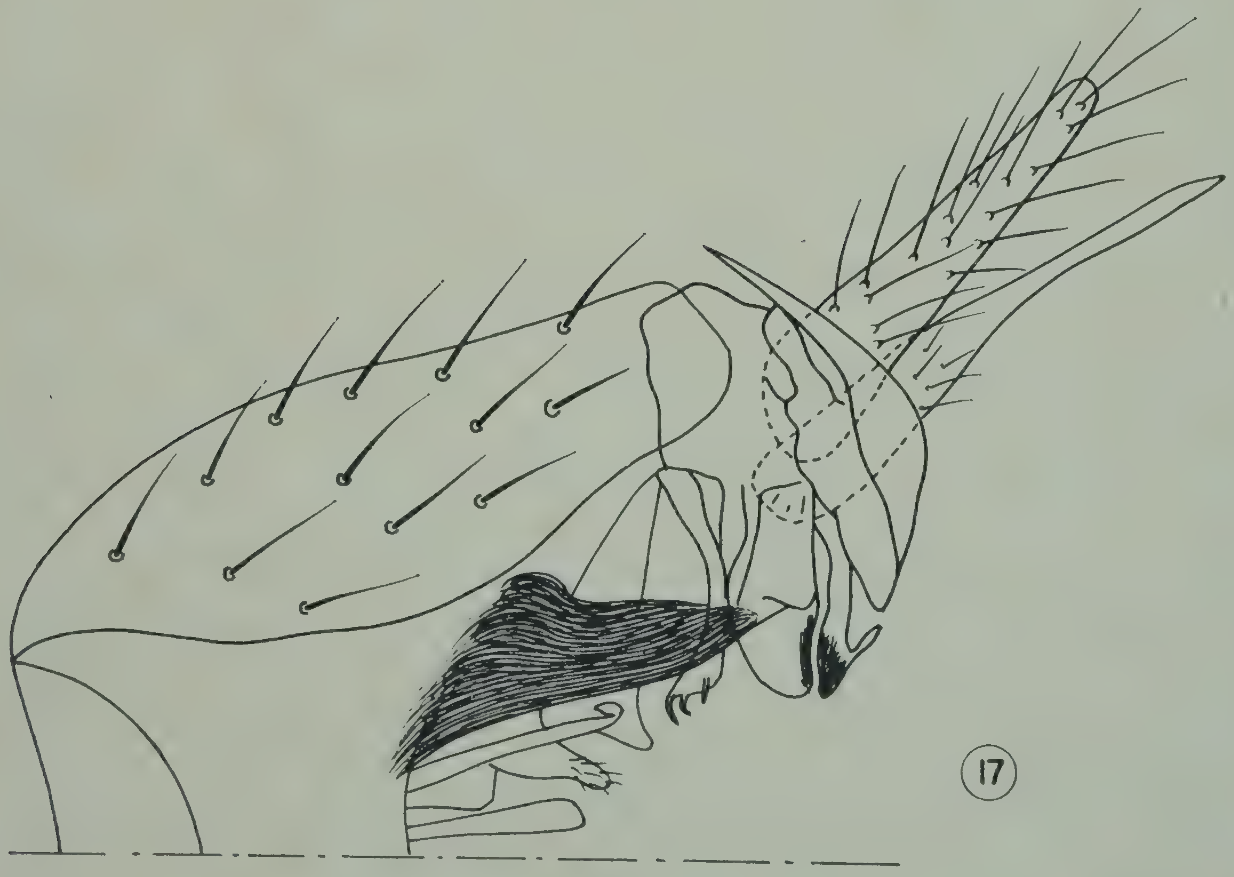

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Figs. 14, 16, 17. Male genitalia, dorso-ventral view. Fig. 15, Wing. 14A, 14B, 14C, M. (A.) *tapuiai* n. sp. 15, 16, M. (A.) *tucumana* n. sp. 17, *Allodia argentinensis* n. sp.

Mycetophila (Abmyceta) flexiseta Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 105.

Distribution. Twelve specimens. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (Abmyceta) forattini Lane, 1951

1951. Lane, Trans. R. Ent. Soc. London, 106: 407.

Distribution. Two specimens. Prov. de Salta, Urundel, II. 1950; Tartagal, II. 1950 (R. Golbach col.).

Mycetophila (?Abmyceta) lacuna Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 123.

Distribution. One specimen. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (Abmyceta) pectinata Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 125.

Distribution. Two specimens. Terr. Santa Cruz, Lago Argentino, II. 1953 (Willink col.); Prov. Tucumán, Quebrada Cainzo, XII. 1950 (R. Golbach col.).

Mycetophila (Abmyceta) pellucida Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 103.

Distribution. Three specimens. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (Abmyceta) spinosa Freeman, 1951

1951. Freeman, Dipt. Pat. & S. Chile, 3: 129.

Distribution. One specimen. Terr. de Santa Cruz, Lago Argentino, II. 1953 (Willink col.).

Mycetophila (Abmyceta) triordinata Freeman, 1953

1951. *Mycetophila triseriata* Freeman, Dipt. Pat. & S. Chile, 3: 128.

1953. *Mycetophila triordinata* Freeman (n. n.) Rev. Chil. Ent., 3: 40.

Distribution. Six specimens. Prov. de Tucumán, Tafí del Valle, XII. 1947; Aconquija, XII. 1950 (R. Golbach col.).

Allodia argentinensis n. sp.

Male. Head: Mouth parts and palpus yellow. Antenna with yellow scape, torus and most of flagellar segment I, the rest dark brown. Occiput dark brown in the middle, yellowish on the sides.

Thorax: Mesonotum yellowish with hairs and dark brown setae over the disk; a prescutellar brown spot. Scutellum yellowish but dark brown in the middle and on continuation to the prescutellar spot; two marginal setae. Postnotum yellowish but brown in the middle. Pleura yellowish, the pleurotergite darker.

Wing hyaline. Haltere yellowish.

Legs: Coxae yellow. Fore leg missing. Mid leg with yellow femur and tibia, the setae short. Hind leg with yellow femur and tibia, the setae also short. Tibiae with rows of setulae.

Abdomen blackish above and yellowish below.

Genitalia: (Fig. 17). Basistyle with the lobes fused and broader than long. Diststyle with elongate and complex lobes as in Fig. 17. Mesosome not observed. Ninth tergite very short, setose and elongate.

Female. Unknown.

Type. Holotype male. To be returned to the Institute Miguel Lillo, Tucumán, Argentina.

Type locality. Prov. de Tucumán, Tafí del Valle, 12. XII. 1947. (R. Golbach col.).

Note. This species is near *A. complexa* but markings of mesonotum and scutellum as well as genitalic characters separate it from all others.

Allodia similis Freeman, 1951

1951. *Allodia* Freeman, Dipt. Pat. & S. Chile, 3: 92.

Distribution. Prov. de Santa Cruz, Lago Argentino, 25. II. 1952 (W. Willink col.), one specimen.

Allodia complexa Lane, 1948

1948. Lane, Rev. Ent., 19: 234.

Distribution. Prov. de Santa Cruz, Lago Argentino, 25. III. 1952 (W. Willink col.); Prov. de Misiones, Eldorado, 1. X. 1948 and Prov. de Corrientes, B. de Astrada, IX. 1948 (J. P. Duret col.), four specimens.

The Utilization of Morphological, Ecological, and Life History Evidence in the Classification of *Protocalliphora* (Diptera: Calliphoridae)

By Curtis W. Sabrosky
Ent. Res. Br., U.S. Dept. Agric.
Washington, D.C.
and
Gordon F. Bennett
Ontario Research Foundation
Toronto, Ont.

ABSTRACT

The North American species of the blow fly genus Protocalliphora, *whose larvae are obligatory bloodsucking parasites of nestling birds, were revised in 1924 by Shannon and Dobroscky and again in 1948 by David G. Hall. The first revision recognized three species and seven varieties; the second, ten species, three of them new. Difficulties in identifications remained, however, and studies were undertaken by the senior author on the adults and by the junior author on the immature stages, ecology, and life history. The studies were mutually advantageous and significantly complementary, and as a result twenty-one Nearctic species are now recognized, besides limited material suggestive of half a dozen others. The revision and a separate paper on ecology will appear elsewhere.*

The adults have a meager variety of specific characters, making differentiation difficult with the increased number of species known. However, study of adequate series and proper association of sexes and immature stages has made it possible to define characters precisely for each taxon, and to appreciate the distinctiveness of different combinations of characters. Three useful characters—body color, width of frons, and form of the outer forceps—were illustrated and discussed in the talk and also shown in the exhibit prepared by the authors. In color there are two classes of males and three of females. In the male sex there are three general types of frontal width, and three of genital forceps. Various combinations of these characters are specific.

Puparial characters are also significant and useful, both in supporting conclusions reached from adult material and in contributing in a major way to the analysis of complexes of species with similar adults in one or both sexes. The chief characters are the cuticular folds of the stigmal region, spine bands on the ventral surface of the puparium, length of cuticular spines on various surfaces, and length of spines in the prothoracic fringe. Morphological differences have also been found in the few eggs and first and second instar larvae thus far studied.

Life-history studies have also demonstrated differences between species, the most important being habitat preference. In the field study at Algonquin Park, Ontario, during the last six seasons, over 2500 bird nests were examined, and 13 species of Protocalliphora *were recovered, 6 of them being relatively abundant. The evidence indicates that, in general, species of* Protocalliphora *show selective preference for certain habitat levels or strata in their environment. Within a given habitat they will apparently attack any species of bird with young confined to a nest. Other phases of the life history, such as the depth of burrowing by the larvae, the minimum temperature requirements for beginning of adult activity, rate of development of larvae and puparia, and length of adult life, are often quite specific and show adaptation to (1) the physical factors of the preferred environments, and (2) the life histories of the bird species found in those environments.*

Of the 21 Nearctic species of Protocalliphora *thus far recognized, 19 are known from both sexes and the immature stages, and 2 from both sexes but no immatures. The harmonizing of evidence from morphological, ecological, and life-history studies, and especially the critical study and correlation of long series of reared specimens with associated immature stages, are assurance that true biological species are involved rather than merely varieties or ecological races. It is seldom indeed that taxonomists have such varied information on which to base revisionary taxonomic work.*

DISCUSSION

H. H. Ross. How many species of *Protocalliphora* occur in other parts of the world, and have these been investigated by the methods that you have used?

C. W. Sabrosky. Five species are recognized in Eurasia; knowledge of them is based on collected adults.

F. A. Urquhart. Are larvae found in the nests of birds that inhabit banks of earth?

G. F. Bennett. Yes, larvae of at least two species occur with such birds.

P. H. Arnaud. How large a population of *Protocalliphora* may occur in one nest? How do the larvae feed?

G. F. Bennett. We found 970 in one nest, but the number varies greatly. The larvae attach themselves to the birds only during the brief periods of actual feeding.

Biosystematics as Applied to the Cecidomyidae

By H. F. Barnes
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ABSTRACT

The object of this communication is to draw attention again to the usefulness of this type of systematic research by describing the methods used and by dealing briefly with some current projects at Rothamsted Experimental Station.

Material of the midges to be tested is obtained by means of surveys and by having garden plots in which the possible host plants are grown. Detector cages are employed to indicate what larvae are present. Emergence pots, kept in an unheated insectary, provide the midges that are then used in intermating experiments and for host plant trials.

By these means a new Contarinia *pest of Shasta Daisy has recently been proved to be* C. chrysanthemi *Keiffer, previously only recorded from wild Ox-eye Daisy, while, in addition, another potential midge pest of Shasta Daisy has been discovered.*

The presence of the White Clover Flower Midge (D. gentneri *Pritchard) has been established in England and Germany. Tests by the author and Mr. D. L. Milne confirm the validity of its separation from the Red Clover Seed Midge* (D. leguminicola *Lintner).*

The Mayetiola *species on cereals and grasses are being tested by Miss Barbara Stokes and preparations are being made to investigate Sorghum gall midges from different countries.*

Brief mention is made of the completion of Miss Stokes' investigation into the Swede Midge and of Dr. R. S. Pitcher's work on the Thomasiniana *species of roses and fruit trees. Finally Mr. W. Nijveldt's studies of the aphid-eating species of* Phaenobremia *are also noted.*

At the Eighth International Congress of Entomology in Stockholm I read a paper (Barnes, 1950) in which the necessity for biological investigations in order to obtain correct specific determination of Cecidomyidae or gall midges was emphasised. Shortly afterwards (Barnes, 1953a) I summarised what had been done during the previous quarter of a century and indicated some immediate problems that awaited solution.

In this contribution I wish to draw attention again to the usefulness of this type of systematic research: first, by describing the methods used; secondly, by dealing briefly with some current lines of investigation at Rothamsted Experimental Station; and lastly, by referring to what has been done since the publication of my last paper (*loc. cit.*) on this subject.

METHODS OF OBTAINING THE INSECT MATERIAL

Larval material is collected in the field, frequently by setting up garden plots of the plants involved and also by means of surveys.

Collection in the Field

In the case of insect pests, material is usually sent in by growers and/or by advisory entomologists. But in order to obtain material of closely allied gall midge species living on weeds, it is often necessary to do a considerable amount of field searching and collecting before sufficient material is obtained for biological experimentation.

Garden Plots

As soon as possible rows of the possible host plants (crops and weeds) of the midges to be tested are established in a garden plot situated conveniently near both the insectary where emergence of the midges is to take place and the glasshouses where the testing will be carried out.

If the gall midges to be tested are endemic in the neighbourhood the plants in these plots soon become infested, thus providing material for the experiments and, in some instances, a clear-cut demonstration of the host plant range of one or other of the gall midges in question.

Botanic gardens and nursery gardens have more than once in the past indicated the host plant range of a gall midge. Thus, on the rockery in Kew Gardens it was obvious that all the species of the subgenus *Euarabis* and none of the other subgenera of *Arabis* were infested by the Arabis Midge, *Dasyneura alpestris* de Meijere. On another occasion in a heather nursery it was only the varieties of *Erica carnea* that attracted the attention of *Wachtliella ericina* F. Loew.

Surveys

Requests are sent out to numerous entomologists and in some instances to non-entomologists in as many counties as possible throughout the country (British Isles), asking them to collect and send in, say, 100 heads of a particular grass or plant gathered in their own district but without explaining the type of damage the particular insect causes. In this manner somewhat random samples, that indicate the distribution of the midge and provide material for experiment, are received. The samples are either examined for the incidence of larval infestation and/or are retained in order to obtain adult material.

On receipt at the laboratory the samples are placed in detector cages (Fig. 1) which consist of lamp glasses standing in the necks of jam jars containing ½-1 inch of water. The top of the lamp glass is covered with a square of glass (2 x 2 slide glasses are very convenient) or with an iron ring covered with muslin. The plant material is put in the swollen part of the lamp glass.

If gall midge larvae that after feeding complete their development in the soil are present, they are soon detected in the water in the jam jar. If only knowledge of their presence or absence is required they are examined and recorded. If on the other hand they are required for rearing adults the lamp glass containing the plant material is inserted in the top of the lamp glass used in the emergence cages (see below). Further larvae can be expected to leave the plant material and fall on to the fibre that is used instead of soil. The larvae already found in the water can also be placed on the fibre as they are not injured by being in water; at any rate submersion in water for not more than 12 hours does not seem to have any effect on their viability.

REARING AND TESTING TECHNIQUES

Emergence

It is always the aim to collect larval material as near to completion of feeding as possible. The infested plant material is then placed in an emergence cage. This consists of a muslin-covered iron ring over the top end of a lamp glass embedded in the soil-and-sand mixture contained in a small flower-pot standing in a saucer. The fibre is firmly pressed down in the lamp glass in order to prevent the midges subsequently emerging becoming entrapped in air spaces and being unable to reach the surface safely. The soil and fibre in the pots is kept damp by watering via the saucer once or twice during the winter months and roughly once a week during the hotter periods of the summer. In March the fibre in the lamp glasses is stirred up, thoroughly moistened and pressed down again. At the same time the lamp glasses are cleaned to enable the emerging midges and parasites to be seen easily, the paper labels inside are checked for legibility, and the iron rings are re-covered if the muslin has perished.

These cages are kept in an unheated insectary out of direct sunlight as far as possible. The insectary at Rothamsted Lodge has proved most successful in that the variety of gall midges placed in it has without exception emerged just at the season of the year when the same species of gall midges have emerged outside under field conditions. This has held good whether the winter or summer has been passed as larvae in the soil and the midges have emerged in the spring, summer or autumn. This insectary is the west end of an old thatched barn. The lateral wood planking on the end and north and south sides has been replaced by anti-sparrow meshed wire netting. The east end joins the insectary on to the rest of the barn. A feature is its height which no doubt is partly responsible for good air circulation. A wind-break, a few inches wide, has been constructed so as to protect the lamp glasses of the emergence cages that are placed on slatted shelves round the sides of the insectary. Additional shelving has been provided in the centre.

Intermating

Mating tests between midges, e.g. individuals reared from different host plants or localities, are carried out either in glass tubes or in small muslin or celophane cages. Occasionally such tests are conducted in the cages, described below, in which it is hoped to breed the next generation of midges.

Breeding Cages

These consist simply of a flower-pot of suitable size for growing the host plant of the midge in a mixture of soil, peat, and sand, standing in a saucer and covered with a muslin cage supported by bamboos. Occasionally it is desirable to have a second muslin cage fixed about an inch away from the inner one, so as to prevent oviposition by extraneous midges, particularly aphid-eating species, through the muslin cage on to the plant inside at points where cage and plant touch.

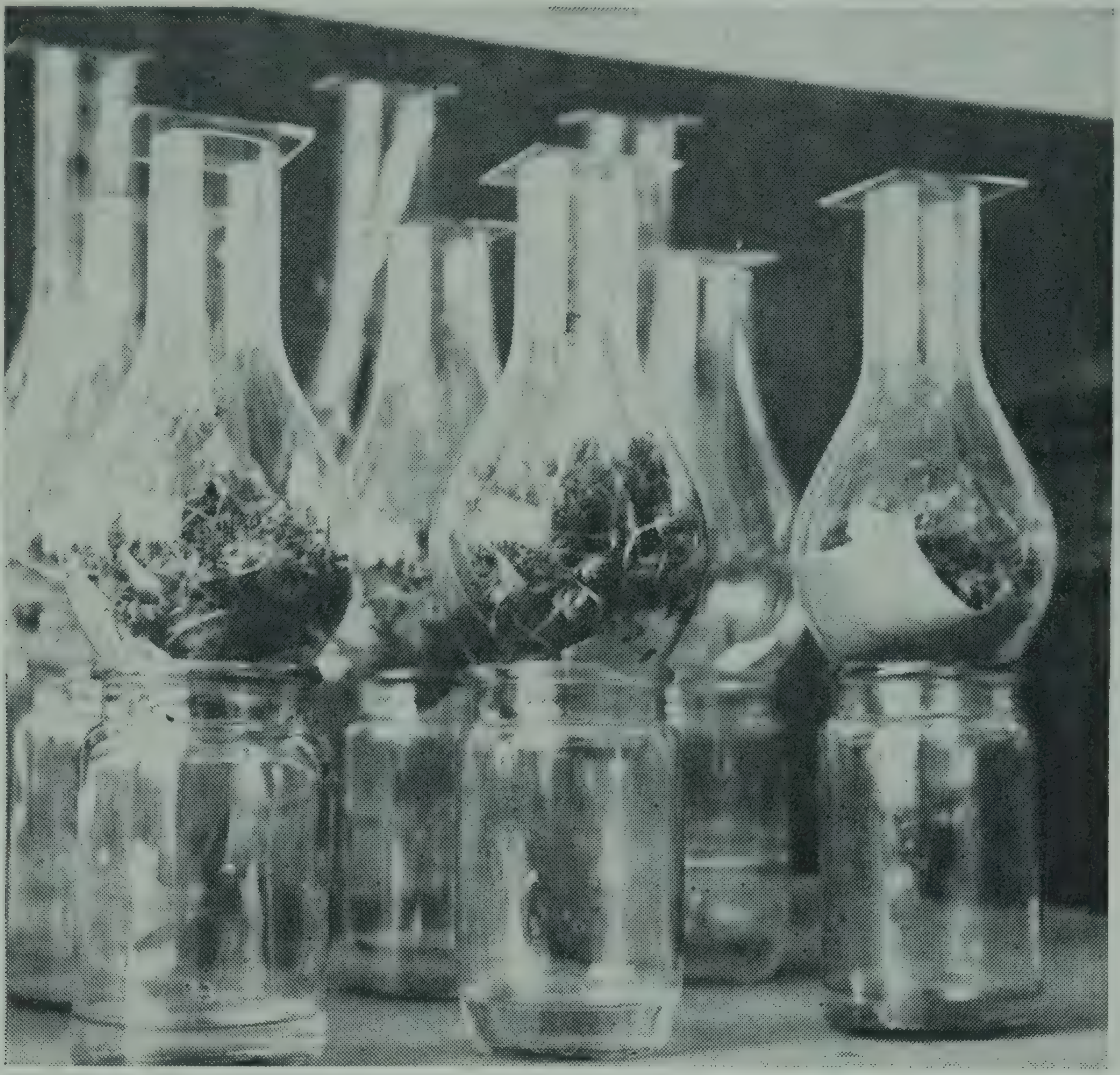


Fig. 1. Detector cages used in connection with surveys.

The midges to be bred are inserted through an incision in the muslin that is kept plugged with cotton wool. Observation is kept to see whether oviposition proceeds.

These breeding cages are maintained in glasshouses that are kept as close to outside temperatures as possible by keeping all the windows open and damping down in hot weather. The glass roof is also summer-misted. All openings are muslin-covered. Alternatively the cages are placed in large cages consisting of a glass roof and anti-sparrow meshed wire netting on the sides.

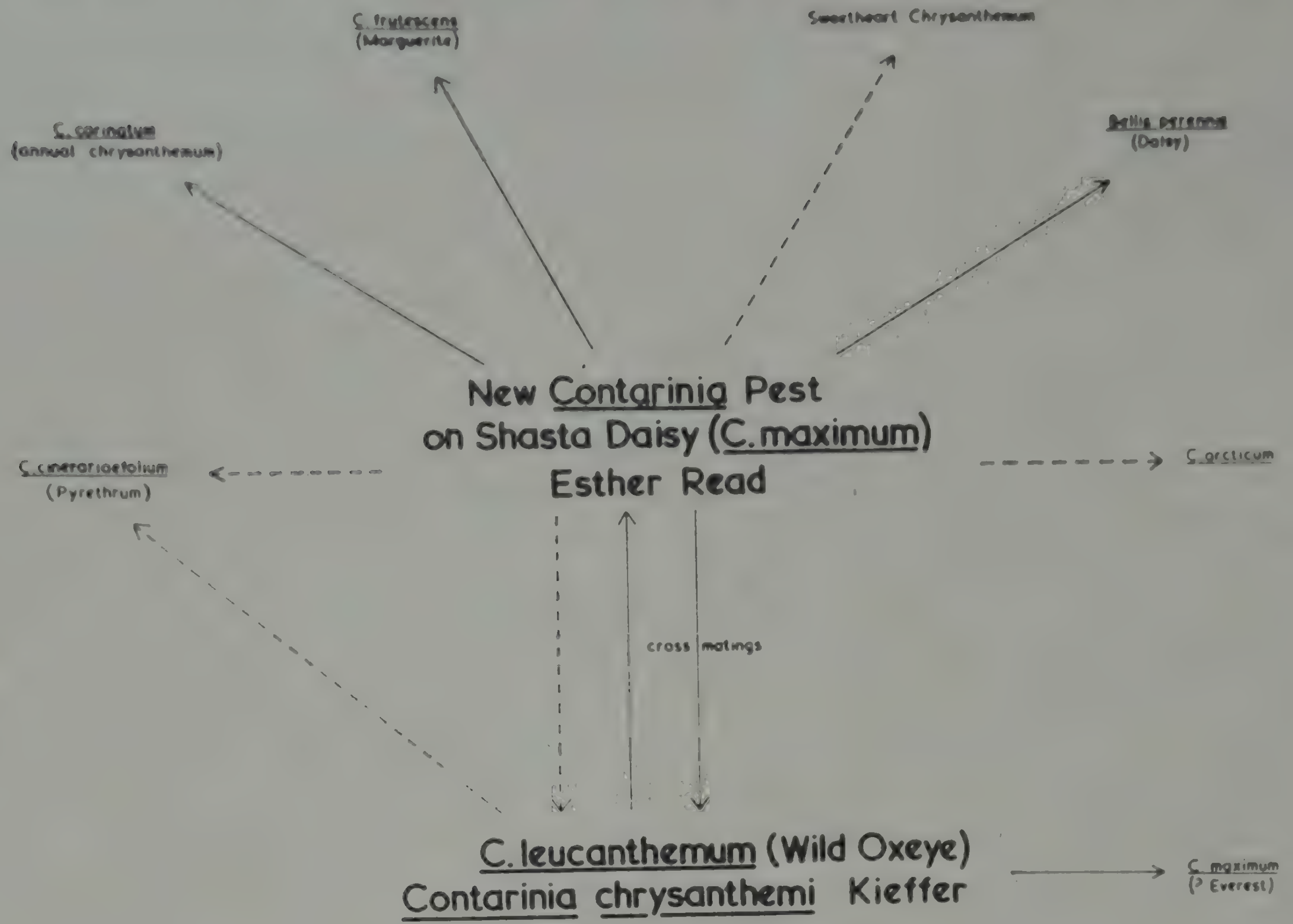
After the insertion of the midges, the plants are watered solely via the saucer.

The midges are reared on the plant species or variety on which they were originally found and also tested as to whether or not they will breed as successfully on other plants and varieties.

HOW THE SHASTA DAISY *CONTARINIA* WAS PROVED TO BE *C. CHRYSANTHEMI* KIEFFER

In the summer of 1951 a new insect pest of Shasta Daisy (*Chrysanthemum maximum* Raymond), var. Esther Read, occurred in the north of England. Examination of the larvae that were found in the malformed flower-buds showed that a *Contarinia* species of gall midge was responsible. The problem was to discover what species it was.

The only records of a *Contarinia* species on the genus *Chrysanthemum* were the description of *C. leucanthemi* Keiffer which had been reported during 1895 in the flowers of *C. leucanthemum* in Lorraine and a note by Bagnall & Harrison of its occurrence in the flowers of wild Ox-eye Daisy (*C. leucanthemum*) in Devon.


C. frutescens
(Marguerite)
Sweetheart Chrysanthemum
C. carinatum
(annual chrysanthemum)
Bellis perennis
(Daisy)
New Contarinia Pest
on Shasta Daisy (C. maximum)
Esther Read
C. cinerariaefolium
(Pyrethrum)
C. arcticum
cross matings
C. leucanthemum (Wild Oxeye)
Contarinia chrysanthemi Kieffer
C. maximum
(? Everest)

2

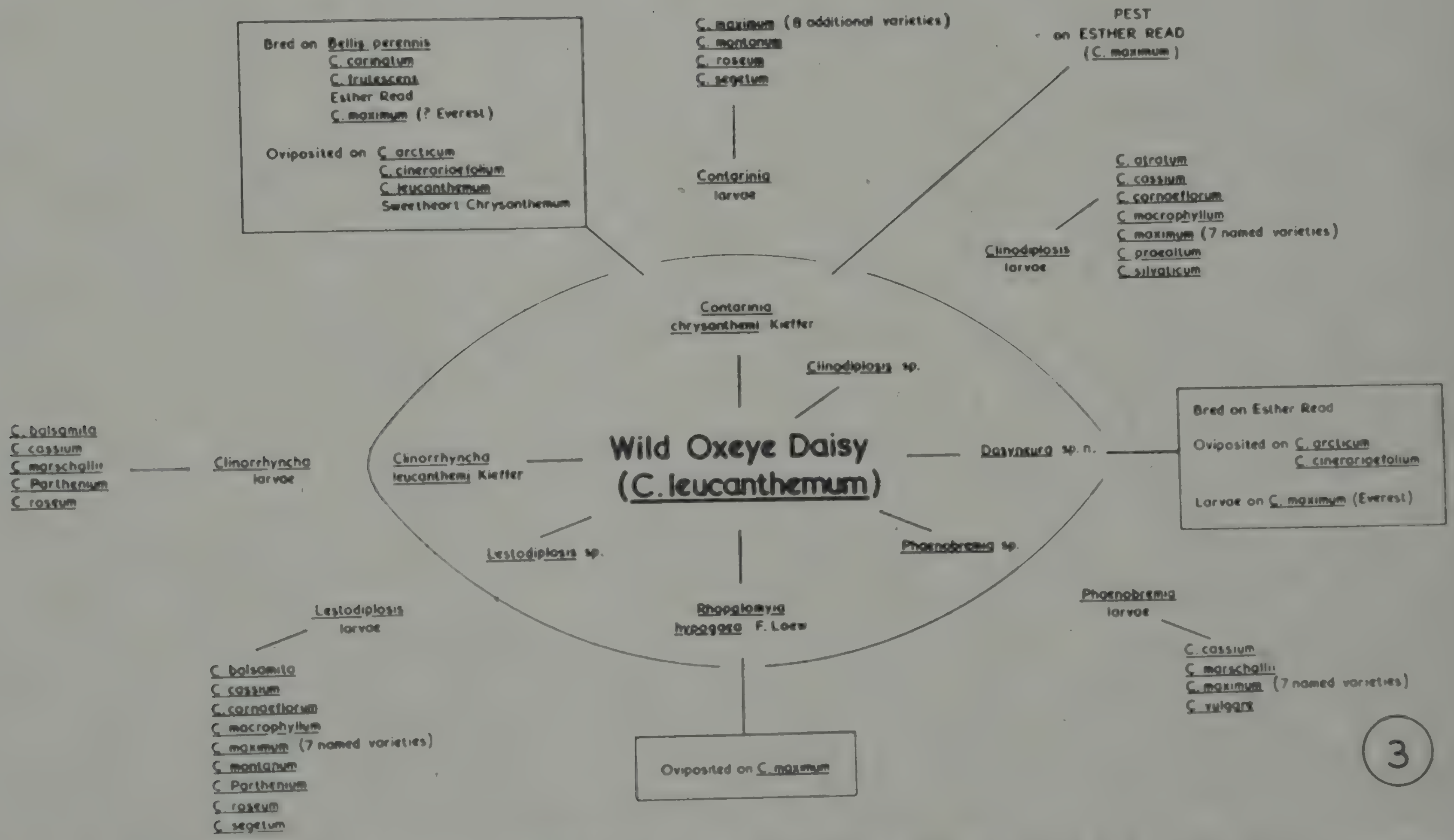

Bred on Bellis perennis
C. carinatum
C. frutescens
Esther Read
C. maximum (? Everest)
Oviposited on C. arcticum
C. cinerariaefolium
C. leucanthemum
Sweetheart Chrysanthemum
C. maximum (8 additional varieties)
C. montanum
C. roseum
C. segetum
Contarinia
larvae
PEST
on ESTHER READ
(C. maximum)
C. atratum
C. cassium
C. corneaeflorum
C. macrophyllum
C. maximum (7 named varieties)
C. praealtum
C. silvaticum
Clinodiplosis
larvae
Contarinia
chrysanthemi Kieffer
Clinodiplosis sp.
C. balsamita
C. cassium
C. marschallii
C. Parthenium
C. roseum
Clinorrhyncha
larvae
Clinorrhyncha
leucanthemi Kieffer
Wild Oxeye Daisy
(C. leucanthemum)
Dasyneura sp. n.
Bred on Esther Read
Oviposited on C. arcticum
C. cinerariaefolium
Larvae on C. maximum (Everest)
Lestodiplosis sp.
Phaenobremia sp.
Lestodiplosis
larvae
Rhopalomyia
hypogaea F. Loew
Phaenobremia
larvae
C. balsamita
C. cassium
C. corneaeflorum
C. macrophyllum
C. maximum (7 named varieties)
C. montanum
C. Parthenium
C. roseum
C. segetum
C. cassium
C. marschallii
C. maximum (7 named varieties)
C. vulgare
Oviposited on C. maximum

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Fig. 2. Diagram illustrating the host plant tests of the *Contarinia* species of Esther Read and C. *leucanthem* Kieffer of wild Ox-eye Daisy.

Fig. 3. Diagram showing the gall midge fauna of wild Ox-eye Daisy and other *Chrysanthemum* species (obtained from the surveys) and the results of the biological tests of certain midge species.

Accordingly a stock of the larvae on Esther Read was obtained. When the midge emerged the following year (1952) tests of its host plant range were made. The results are shown in Fig. 2. The females oviposited readily on C. *arcticum*, C. *carinatum* (annual chrysanthemum), C. *cinerariaefolium* Vis. (insecticide pyrethrum), C. *frutescens* Thunb. (Marguerite or Paris Daisy), C. *leucanthemum* (wild Ox-eye Daisy) and on Sweetheart chrysanthemum. The next year adults were reared from the C. *carinatum* and C. *frutescens*. In addition in a later year this midge was also proved to be able to reach the adult stage on *Bellis perennis*.

While these host plant tests were being carried out, a garden plot containing various species of *Chrysanthemum* was being established at Rothamsted Lodge. Unfortunately none of these plants became infested. A survey, on the lines previously described, was also started in order to obtain material of *C. chrysanthemi* Kieffer from wild Ox-eye Daisy. The result of this is shown in Fig. 3. Besides *C. chrysanthemi* Kieffer larvae being found to occur in many localities, three other primary gall midges were recorded as well as an inquiline *Clinodiplosis*, a predatory *Lestodiplosis* and an aphid-eating *Phaenobremia*. The primary species were an undescribed *Dasyneura*, *Clinorrhyncha leucanthemi* Kieffer and *Rhopalomyia hypogaea* F. Loew.

As a result a good stock of *C. chrysanthemi* was obtained with the result that in the next year (1953) it was possible to carry out intermating tests between the midge of Esther Read and that of wild Ox-eye Daisy. It was demonstrated that the *Contarinia* of Esther Read would mate just as readily with *C. chrysanthemi* reared from wild Ox-eye Daisy as it would with individuals from Esther Read and vice versa. These matings were shown to be fertile by rearing the G_1 on wild Ox-eye Daisy.

Further host plant tests demonstrated that *C. chrysanthemi* Kieffer from wild Ox-eye Daisy would breed readily on Esther Read and oviposit freely on *C. cinerariaefolium* and *C. maximum*.

In this manner it was proved that the new gall midge pest of Esther Read was none other than *C. chrysanthemi* Kieffer which was widely distributed throughout the country on wild Ox-eye Daisy.

The study was closed after a preliminary survey of the gall midge fauna of *Chrysanthemum* species growing in certain botanic gardens had been made (see also Fig. 3). But by this time it had been demonstrated that the undescribed *Dasyneura* species of wild Ox-eye Daisy would breed readily on Esther Read and was therefore a potential pest of this cultivated ornamental.

Further information regarding the discovery of *C. chrysanthemi* as a pest of Esther Read is given by Cohen (1952), while details of the biological testing of this pest have also been given (Barnes, 1953b, 1953c).

CURRENT INVESTIGATIONS AT ROTHAMSTED

Mr. D. L. Milne, a Ph.D. (London) student from S. Africa, is now actively pursuing a study of the gall midge fauna of clover flower-heads that I initiated in 1954 (Barnes, 1954). The garden plot and survey methods and the rearing and testing techniques are being used and adapted to fit the particular problems. The presence of the White Clover Flower Midge (*Dasyneura gentneri* Pritchard) in England and Germany has been established; while tests are confirming the validity of its separation from the Red Clover Seed Midge (*D. leguminicola* Lintner). Efforts are also being made to ascertain the role played by gall midges of other genera that also occur in clover flower- and seed-heads.

Miss Barbara M. Stokes, a member of the entomology department, is making a special study of the *Mayetiola* species that occur on cereals and grasses and hopes to test the validity of some of the score or so species that have been described from various grasses in Europe. Her first contribution on this subject has been prepared for publication in the *Annals of applied Biology* (Stokes, 1957).

A third line of investigation concerns the gall midge fauna, especially *Contarinia sorghicola* Coq., of sorghum and other millet heads. The necessary biological testing of the closely allied species occurring in any particular area or country should be carried out within that area or country. But it is important to discover if the midges in one country are identical with those occurring in another: for example, in order to settle the vexed question as to the identity of the Indian sorghum midge known as *S. caudata* Felt (Barnes, 1956). Whereas it would be extremely unwise to import living midge material from one sorghum- and millet-growing country to another, the necessary biological testing of the species from different countries could be done with safety in a country where sorghum and millets are not grown. It has already proved possible to emerge sorghum midge from the Gambia at Rothamsted, so infested material under licence has been obtained from India and West Africa. It is hoped to carry out inter-mating tests. Later, when it has been found possible to grow sorghum and other millets so that they are in the correct stage of growth for oviposition when the midges are available, it is hoped to complete their biosystematic testing.

OTHER INVESTIGATIONS

Miss Barbara M. Stokes has completed her studies of the *Contarinia* species living on the Cruciferae in England and the Netherlands (Stokes, 1953a, 1953b). Her biological investigations have proved that *C. nasturtii* Kieffer, *C. isatidis* Rübsaamen and *C. ruderalis* Kieffer are but one species. The latter two therefore were relegated to the synonymy of *C. nasturtii*. The host plant range of this species, already known to be extensive, was further increased by 14 additional plant species, of which 8 were established by experiment and 6 by including known host plants of *C. ruderalis*. Three further host plants have been added by Miss Stokes' experiments in Holland that have been appraised by Leefmans (1953).

The biological studies of the *Thomasiniana* species of roses and fruit trees made by Dr. R. S. Pitcher of East Malling Research Station have now been largely published (Pitcher, 1954, 1955a, 1955b).

Finally W. Nijveldt of the I.P.O., Wageningen, is actively pursuing his biosystematic studies of certain aphid-eating *Phaenobremia* species and already publication of his results has started (Nijveldt, 1954 and 1955). It seems quite certain now that *Phaenobremia* species are somewhat polyphagous and by no means restrict their food to single aphid species.

REFERENCES

Barnes, H. F. 1950. The need for biological investigations in the specific determination of gall midges. *Proc. 8th Int. Congr. Ent.*, Stockholm 1948: 106–10.

Barnes, H. F. 1953a. The biological approach to the species problem in gall midges (Dipt., Cecidomyidae). *Ann. ent. fenn.* 19: 2–24.

Barnes, H. F. 1953b. The Shasta Daisy Midge and other insects in flowers of *Chrysanthemum* species. *Plant Path.* 2: 52–3.

Barnes, H. F. 1953c. Investigations into the gall midges of chrysanthemum flowers, 1951–53. *Entomologist* 86: 292–7.

Barnes, H. F. 1954. Gall midges living in white clover flowers. *Entomologist* 87: 257–64.

Barnes, H. F. 1956. Gall midges of economic importance. Vol. VII. Gall midges of cereal crops. London: *Crosby Lockwood & Son, Ltd.* 261 pp.

Cohen, M. 1952. *Contarinia chrysanthemi* Kieffer—a new gall midge pest of Shasta Daisy. *Plant Path.* 1: 51–3.

Leefmans, S. 1953. Enige notities naar aanleiding van het artikel van Miss Barbara Stokes. *Tijdschr. PlZiekt.* 59: 91–4.

Nijveldt, W. 1954. The range of prey of *Phaenobremia urticariae* Kffr. and *Ph. aphidivora* Rübs. (Diptera, Itonididae). *Ent. Ber.* 15: 207–11.

Nijveldt, W. 1955. Additional notes on my paper on the range of prey of *Phaenobremia aphidivora* Kffr., and *Ph. urticariae* Rübs. [*sic*] (Diptera, Itonididae). *Ent. Ber.* 15: 436–7.

Pitcher, R. S. 1954. The host plant range and economic importance of a group of gall midges (*Thomasiniana* spp.) associated with fruit. *Rep. E. Malling Res. Sta.* 1953, 168–70.

Pitcher, R. S. 1955a. A comparison of a group of gall midges of the genus *Thomasiniana* Strand, E., 1916 and a description of a new species from wild blackberry. *Bull. ent. Res.* 46: 27–38.

Pitcher, R. S. 1955b. The larval instars of some gall midges of the genus *Thomasiniana* Strand, E., 1916 (Diptera: Cecidomyidae). *Proc. R. ent. Soc. Lond.*, A. 30: 97–102.

Stokes, Barbara M. 1953a. Biological investigations into the validity of *Contarinia* species living on the Cruciferae, with special reference to the Swede Midge, *Contarinia nasturtii* (Kieffer). *Ann. appl. Biol.* 40: 726–41.

Stokes, Barbara M. 1953b. The host plant range of the Swede Midge (*Contarinia nasturtii* Kieffer) with special reference to types of plant damage. *Tijdschr. PlZiekt.* 59: 82–90.

Stokes, Barbara M. 1957. Observations and experiments on the Hessian Fly (*Mayetiola destructor* Say). *Ann. appl. Biol.* 45: 122–32.

DISCUSSION

W. A. Reeks. How much work has been done on the cecidomyids of conifers in England? Also, what precautions are taken against moulds developing in the medium for pupation?

H. F. Barnes. Virtually no work has been done on the cecidomyid fauna of conifers in England. Ordinary bulb fibre is used for pupation, because moulds apparently do not develop in it. Emergence cages set up in 1939 still show no sign of mould, although algae grow in them, for the fibre has remained moist.

Les *Derolus* Africains (Coleoptera: Cerambycidae)

Par P. Lepesme et S. Breuning
Paris, France

RÉSUMÉ

Ce genre comprend d'Afrique 33 espèces que l'on pourra déterminer à l'aide du tableau dichotomique. Des descriptions des différentes espèces sont également données, ainsi que la distribution géographique de chacune.

Dans la tribu des Cerambycini (Cerambycidae Cerambycinae), le genre *Dérolus* est remarquablement caractérisé par ses trois paires de fémurs pourvus d'une fine, mais très nette, carène longitudinale.

Ce genre est réparti dans les régions paléarctique, indomalaise et éthiopienne. Il comprend à ce jour, d'Afrique, après l'étude des AA. 33 espèces que l'on pourra déterminer à l'aide du tableau dichotomique dressé par ceux-ci. Des descriptions des différentes espèces sont également données, ainsi que la distribution géographique de chacune.

DEROLUS GAH.

Pachydissus (Derolus) Gahan, 1891, Ann. Mag. Nat. Hist. (6) VII, p. 26.
Capnocerambyx Reitter, 1894, Ent. Nachr. XX, p. 356.
Derolus Gahan, 1906, Fauna Brit. India, Col. I, p. 185.

Parmi les Cerambycidae, Cerambycinae, Cerambycina de la tribu des Cerambycini, le genre *Derolus* est un des mieux caractérisés par l'absence d'une épine latérale sur le pronotum et surtout par la nette carêne longitudinale dont sont pourvus tous ses fémurs sur la face externe.

Il groupe d'élégants longicornes allongés à très allongés dont la livrée est beige à brun uniforme ou comporte des bandes ou taches brunes sur fond clair ou claires sur fond brun.

On ne connaît rien de leur biologie si ce n'est qu'en Afrique du Nord *D. mauritanicus* Buq. effectue son développement dans les tiges de Laurier-rose de faible diamètre.

Le genre est dispersé dans toute la région paléarctique, la région indomalaise et surtout la région éthiopienne où l'on dénombre actuellement, après la révision ci-dessous, 33 espèces que l'on pourra séparer à l'aide du tableau suivant:

Tableau des sous-genres et espèces

1. Pronotum lisse, ni ponctué ni ridé .... Sg. *Microderolus* Auriv.
– Pronotum densément ponctué ou ridé 2
2. Pronotum ponctué, mais non ridé .... Sg. *Dissaporus* Auriv.
– Pronotum nettement ridé 3
3. Troisième article des antennes étiré en une épine apicale interne .... Sg. *Spiniderolus* Lep. et Breun.
– Troisième article des antennes non étiré en une épine apicale 4
4. Fémurs postérieurs pédonculés .... Sg. *Graciliderolus* Lep. et Breun.
– Fémurs postérieurs claviformes .... Sg. *Derolus* Gah. s. s.

Sg. *Derolus* Gah. s. s.

1. Les premiers articles antennaires frangés en dessous 2
– Les premiers articles antennaires non frangés en dessous 6
2. Elytres arrondis à l'apex 3
– Elytres échancrés à l'apex 5
3. Elytres très densément ponctués .... *lepautei* Lep.
– Elytres imponctués 4
4. Elytres couverts d'une pubescence soyeuse formant des taches nuageuses .... *gyllenhali* Fahr.
– Elytres couverts d'une pubescence uniforme brun gris .... *arnoldi* Lep. et Breun.
5. Elytres imponctués .... *basilewskyi* Lep. et Breun.
– Elytres très finement ponctués dans la moitié antérieure .... *ivorensis* Lep. et Breun.
6. Elytres échancrés à l'apex (l'angle apical marginal étiré en un lobe triangulaire pointu) 7
– Elytres arrondis ou tout au plus faiblement tronqués à l'apex 8
7. Elytres couverts d'une fine pubescence brun grise .... *femorellus* Chevr.
– Elytres couverts d'une dense pubescence rouge doré à reflets soyeux .... *fulvus* Jord.

8. Elytres rouges et couverts sur les deux tiers antérieurs d'une dense pubescence dorée uniforme .... *aureus* Lep. et Breun.
– Elytres jamais couverts d'une pubescence semblable 9
9. Elytres rouge clair avec des bandes plus sombres 10
– Ornementation des élytres différente 13
10. Elytres faiblement mais nettement tronqués à l'apex .... *dilatatus* Chevr.
– Elytres arrondis à l'apex 11
11. Pronotum faiblement strié en travers .... *cinctus* Jord.
– Pronotum profondément strié 12
12. Disque du pronotum strié en travers .... *subcinctus* Lep. et Breun.
Disque du pronotum irrégulièrement et vermiculeusement strié .... *vagevittatus* Lep. et Breun.
13. Robuste; fémurs très faiblement carénés .... *incultus* Gerst.
– Elancé; fémurs très nettement carénés 14
14. Elytres avec une étroite bande transversale prémédiane ondulée jaune .... *kraatzi* Jord.
– Elytres sans une bande semblable 15
15. Chaque élytre avec une large bande longitudinale discale argentée ou dorée 16
– Elytres ans une bande semblable 17
16. Disque du pronotum avec une dépression nette en fer à cheval .... *ptycholaemoides* Lep. et Breun.
– Disque du pronotum sans une dépressions semblable .... *ruandae* Lep. et Breun.
17. Elytres couverts d'une pubescence uniforme sans reflets soyeux 18
– Elytres couverts d'une pubescence soyeuse, formant selon la lumière des taches nuageuses 22
18. Disque du pronotum faiblement strié en travers et pourvu d'une dépression nette en fer à cheval .... *brunneipennis* Gah.
– Disque du pronotum profondément strié mais sans dépression en fer à cheval 19
19. Quart basilaire des élytres peu finement ponctué .... *martini* Lep. et Breun.
– Quart basilaire des élytres tout au plus très finement ponctué 20
20. L'angle apical sutural de l'élytre arrondi; disque du pronotum orné de taches dorées .... *parus* Jord.
– L'angle apical sutural de l'élytre étiré en une petite épine; disque du pronotum sans taches dorées 21
21. Moitié antérieure du disque du pronotum pourvu de deux rides circulaires .... *bifarius* Duffy
– Disque du pronotum sans rides circulaires .... *mauritanicus* Buqu.
22. Disque du pronotum profondément strié en travers dans la moitié postérieure et pourvu de deux petits tubercules prémédians .... *subaureus* Jord.
– Disque du pronotum sans tubercules prémédians 23
23. Disque du pronotum profondément strié, mais sans dépression à fer à cheval 24
– Disque du pronotum pourvu d'une dépression nette à fer à cheval 25
24. Elytres arrondis à l'apex .... *malaisei* Lep. et Breun.
– Elytres faiblement mais nettement tronqués à l'apex .... *spurius* Jord.
25. Les deux branches latérales de la dépression en fer à cheval sont peu accusées .... *sulcatus* Auriv.
– Les deux branches latérales de la dépression en fer à cheval sont très nettement accusées 26
26. Elytres arrondis à l'apex .... *arciferus* Gah.
– Elytres faiblement mais nettement tronqués à l'apex .... *pseudaureus* Lep. et Breun.

Sg. *Spiniderolus* Lep. et Breun.

Une seule espèce .... *euparus* Auriv.

Sg. *Graciliderolus* Lep. et Breun.

Une seule espèce .... *gracilis* Lep. et Breun.

Sg. *Dissaporus* Auriv.

1. Disque du pronotum très finement ponctué .... *cachani* Lep. et Breun.
– Disque du pronotum peu finement ponctué 2
2. Chaque élytre pourvu d'une crête longitudinale discale nette .... *mythicus* Gyll.
– Elytres sans crête discale .... *cylindricus* Fahr.

Sg. *Microderolus* Auriv.

Une seule espèce .... *latevittatus* Auriv.

1. SG. *DEROLUS* GAH. (S. S.)

Pachydissus (Derolus) Gahan, 1891, Ann. Mag. Nat. Hist. (6) VII, p. 26.
Capnocerambyx Reitter, 1894, Ent. Nachr. XX, p. 356.

Troisième article des antennes non étiré en une épine apicale, le quatrième article beaucoup moins long que le cinquième; disque du pronotum ridé; fémurs postérieurs claviformes.

Type: *arciferus* Gah.

1. *gyllenhali* Fahr.

Tapinolachnus gyllenhali Fahroeus, 1872, Oervers. Vet. Ak. Förh. XXIX/ 1, p. 52.
Tapinolachnus oatesi Olliff, 1889, Oates, Matabele Land, ed. 2, App., p. 378, Pl. VIII, Fig. 7.
Tapinolachnus gyllenhali Distant, 1904, Ins. Transvaal, p. 112, pl. IX, Fig. 5.

Elancé. Antennes deux fois plus longues que le corps (♂) ou un peu plus longues (♀), les huit premiers articles frangés de poils serrés assez longs, le scape très finement ponctué et ridé. Pronotum un peu plus long que large, le disque densément et assez régulièrement mais peu profondément strié en travers sauf au centre et pourvu d'une faible dépression en fer à cheval. Elytres imponctués, arrondis à l'apex, mais ayant l'angle apical sutural étiré en une petite épine.

Brun foncé, couvert de pubescence gris argenté formant selon la lumière des taches nuageuses.

Long.: 20–25 mm. Type au Musée de Stockhlom.

Décrit par Fahroeus sur des individus de Caffrérie; *oatesi* Oll. est un synonyme.

Transvaal: Rustenburg, IX–X–94, leg. Ayres (Muséum de Paris); South Rhodesia: Mt. Gelinde, leg. R. Stevenson, XII–44 (coll. Hunt); Tanganyika: Luitpoldkette (Muséum de Paris); Lukuledi (Inst. Roy. Sc. Nat. Belgique); Tununguo, ex coll. Clermont (Musée de Tervueren).

2. *arnoldi* n. sp.

Assez élancé. Antennes un peu plus longues que le corps (♀), les sept premiers articles frangés de poils serrés assez longs, le scape très finement ridé. Pronotum un peu plus long que large, pourvu d'une profonde dépression postmédiane en fer à cheval. Elytres imponctués, arrondis à l'apex, mais ayant l'angle apical sutural étiré en épine.

Brun foncé, couvert d'une assez dense pubescence uniforme brun gris.

Long.: 26 mm.

Type: 1 ♀ de Southern Rhodesia: Khami, 25–XI–50 au Southern Rhodesian Museum de Bulawayo.

3. *lepautei* Lep.

Derolus lepautei Lepesme, 1947, Bull. Soc. ent. France, p. 152.

Assez robuste. Antennes à peine plus longues que le corps, les six premiers articles frangés en dessous de poils peu serrés et peu longs, le scape très densément et peu finement ponctué. Pronotum aussi long que large, densément et assez profondément ridé en travers. Elytres arrondis à l'apex et pourvus d'une ponctuation extrêmement dense et très fine.

Brun foncé couvert d'une fine pubescence brun jaunâtre.

Long.: 16 mm. Type in coll. Lepesme.

Décrit par Lepesme sur un individu de Mauritanie: Port Etienne.

4. *ivorensis* n. sp.

Elancé. Antennes à peine de moitié plus longues que le corps (♂) ou aussi longues (♀), les six premiers articles frangés de poils peu serrés et assez courts, le scape très densément et très finement ponctué. Pronotum un peu plus long que large, peu densément mais profondément ridé en travers et pourvu de deux rides longitudinaux rapprochés de la ligne médiane, ces deux rides réunis en un seul sur le tiers antérieur. Elytres densément et très finement ponctués dans la moitié antérieure, échancrés à l'apex (l'angle sutural étiré en une petite épine, l'angle marginal en un lobe triangulaire pointu).

Brun rougeâtre couvert de pubescence soyeuse dorée. Pronotum orné de quatre étroites bandes longitudinales brun foncé, les deux internes soudées en une seule dans le tiers antérieur.

Long.: 20–26 mm.

Type: 1 ♂ de Côte d'Ivoire: N'Dzida, dans la coll. Lepesme.—Allotype, id.—1 paratype de Côte d'Ivoire, Tristan Lacroix (Muséum de Paris); 1 paratype (♀) de Liberia: Harbel, I–47, leg. H. Beatty (Musée de New York).

5. *basilewskyi* n. sp.

Elancé. Antennes d'un quart plus longues que le corps, les six premiers articles frangés de poils peu serrés et assez courts, le scape densément et finement ponctué. Pronotum aussi long que large, assez densément et profondément strié en travers. Elytres imponctués, échancrés à l'apex (l'angle sutural étiré en une épine mince, l'angle marginal en un lobe triangulaire pointu).

Brun foncé, couvert de pubescence soyeuse dorée, formant sur les élytres selon la lumière des taches nuageuses.

Long.: 26 mm.

Type: 1 ♀ du Congo belge: Lulua: Kapanga, IX–32, leg. G. F. Overlaet, au Musée de Tervúeren.

6. *femorellus Chevr.*

Pachydissus femorellus Chevrolat, 1856, Rev. Zool. (2) VIII, p. 340; 1858, Cent. Long., no. 44.

Pachydissus femorellus Murray, 1870, Ann. Mag. Nat. Hist. (4) VI, p. 44.

Pachydissus (Derolus) femorellus Gahan, 1891, Ann. Mag. Nat. Hist. (6) VII, p. 27.

Derolus tenuis Duvivier, 1891, Ann. Soc. ent. belg. XXXV, Bull. p. CCCLXVII; 1892, Ann. soc. ent. belg. XXXVI, p. 353.

Assez robuste. Antennes de moitié plus longues que le corps (♂) ou à peine plus longues (♀), non frangées, le scape très densément et finement ponctué et ridé. Pronotum aussi long que large, densément, peu régulièrement et profondément ridé en travers. Elytres densément et très finement ponctués dans la moitié antérieure, échancrés à l'apex (l'angle sutural étiré en une assez longue et mince épine, l'angle marginal en un lobe triangulaire pointu).

Brun foncé, couvert d'une fine pubescence brun grisâtre. Tête et pronotum avec des taches dorées vagues. Fémurs d'un rouge assez foncé.

Long.: 22–27 mm. Type au British Museum.

Décrit par Chevrolat sur des individus du Nigeria: Old Calabar.; *tenuis* Duv. est un synonyme.

Sierra Leone, leg. Major Bainbridge (Inst. Roy. Sc. Nat. Belgique); Warri, IV–97, leg. Dr. Roth (Muséum de Paris); Congo belge: Ibembo (Duvivier, Inst. Roy. Sc. Nat. Belgique), Urwald Mawambi, 1910 leg. Grauer (idem).

7. *fulvus* Jord.

Derolus fulvus Jordan, 1903, Novit. Zool. X, p. 137.

Elancé. Antennes un peu plus longues que le corps (♂) ou un peu moins longues (♀), le troisième article presque trois fois plus long que le quatrième, un peu plus long que le cinquième. Pronotum aussi long que large, très grossièrement ridé en travers, peu régulièrement surtout le long de la ligne médiane. Elytres imponctué échancrés à l'apex (l'angle sutural étiré en une très petite épine, l'angle marginal en un lobe triangulaire pointu).

Rouge foncé; tout le dessus du corps, la partie dorsale des pattes et les antennes couverts d'une dense pubescence rouge doré formant sur les élytres selon la lumière des taches nuageuses, le dessous du corps et le restant des pattes à fine pubescence argentée.

Long.: 20–25 mm. Type au Muséum de Paris.

Décrit par Jordan sur des individus de Guinée espagnole: Benito. Congo belge: Sankuru, leg. E. Luja (Musée de Tervueren); Côte d'Ivoire: Adiopodoumé, XI–XII–52 (coll. Lepesme).

8. *dilatatus* Chevr.

(Fig. 1.)

Pachydissus dilatatus Chevrolat, 1856, Rev. Zool. (2) VIII, p. 567; 1858, Cent. Long., no. 60.

Pachydissus dilatatus Murray, 1870, Ann. Mag. Nat. Hist. (4) VI, p. 45.

Derolus dilatatus Jordan, 1903, Novit. Zool. X, p. 135.

Derolus dilatatus Lepesme, 1953, Cat. Col. Ceramb. de Côte d'Ivoire, Pl. VIII, Fig. 3.

Elancé. Antennes d'un quart plus longues que le corps (♂) ou à peine plus longues (♀), le scape très densément et très finement ponctué. Pronotum sensiblement plus long que large, peu profondément et très irrégulièrement ridé. Elytres très faiblement rétrécis dans la partie médiane, faiblement tronqués à l'apex, très densément et très finement ponctués sauf dans la région apicale.

Brun foncé, couvert d'une fine pubescence argentée. Tête et disque du pronotum orné de taches dorées. Elytres rouge clair à fine pubescence soyeuse dorée. Une bande longitudinale peu large le long du bord latéral sauf dans la région apicale et une bande suturale parcourant les deux premiers tiers (très étroite dans le premier tiers, plus large dans le second) brun foncé. Pattes et antennes rouges.

Long.: 12–15 mm. Type au British Museum.

Décrit par Chevrolat sur des individus de Nigeria: Old Calabar. Cameroun: Johann Albrechtshöhe, 1896, leg. C. Conradt, Doumé, 1930, leg. P. Cural (Muséum de Paris); Guinée espagnole: Benito (idem); Côte d'Ivoire: Abengourou, Adiopodoumé (coll. Lepesme) Guinée française: Mt. Nimba (Muséum de Paris).

9. *cinctus* Jord.

Derolus cinctus Jordan, 1903, Novit. Zool. X, p. 136.

Proche de *dilatatus* Chevr., mais plus robuste, les antennes aussi longues que le corps (♂) ou sensiblement moins longues (♀), le pronotum plus large, faiblement ridé en travers dans la moitié postérieure, à peine ridé dans la moitié antérieure, les élytres arrondis à l'apex.

La coloration est semblable, mais la tête et le pronotum ne présentent pas de taches dorées et chaque élytre présente une assez large bande transversale brun foncé, reliant les deux bandes longitudinales.

Long.: 14–18 mm. Type au Muséum de Paris.

Décrit par Jordan sur des individus de Guinée espagnole: Benito. Congo belge: Luki, 1948, leg. C. Denis (Musée de Tervueren): Angola: Lunda, X–46 (coll. Lepesme).

10. *subcinctus* n. sp.

Proche de *dilatatus* Chevr., mais le scape plus éparsément ponctué, le pronotum à peine plus long que large, beaucoup plus régulièrement ridé en travers, les élytres arrondis à l'apex, la tête et le pronotum dépourvus de taches dorées, les deux bandes longitudinales sombres de l'élytre reliée par une bande transversale sombre occupant plus que tout le deuxième tiers.

Long.: 11 mm.

Type: 1 ♂ d'Ubanghi: Yalinga, leg. G. le Testu, ex coll. Maublanc, dans la coll. Lepesme. 1 paratype du Congo belge: Lulua Kapanga, X–32, leg. F. G. Overlaet (Musée de Tervueren).

11. *vagevittatus* n. sp.

Proche de *dilatatus* Chevr., mais le scape moins finement ponctué, le prodonotum plutôt vermiculeusement ridé, les élytres arrondis à l'apex, sans bandes longitudinales sombres, ni latérale ni suturale, mais couverts d'une pubescence rouge doré plus dense à forts reflets soyeux, formant selon la lumière des taches discales nuageuses plus sombres.

Long.: 12 mm.

Type: 1 ♀ du Congo belge: Kasai, 1904, leg. Edm. Taymans, au Muséum de Paris.

12. *aureus* n. sp.

Elancé. Antennes à peu près aussi longues, le scape très densément et finement ponctué. Pronotum un peu plus long que large, finement ridé en travers sur le tiers basilaire, finement et irrégulièrement ridé sur le tiers médian. Elytres subtronqués à l'apex, densément et très finement ponctués.

Brun foncé, couvert d'une fine pubescence grise Pronotum avec deux taches circulaires disco-latérales postmédianes dorées. Elytres rouges, les deux tiers antérieurs courverts d'une dense pubescence uniforme d'un doré vif, le tiers apical à très fine pubescence grisâtre. Sterna revêtus de pubescence argentée.

Long.: 10 mm.

Type: du Congo belge: Mayumbe, Makaia, N–Tete, 24–XI–15, leg. R. Mayné au Musée de Tervueren.

13. *ptycholaemoides* n. sp.

Elancé. Antennes d'un tiers plus longues que le corps (♂) ou aussi longues (♀), le scape très densément et très finement ponctué. Pronotum un peu plus long que large, pourvu d'une profonde dépression postmédiane en fer à cheval. Elytres faiblement tronqués à l'apex, densément et extrêmement finement ponctués sur les trois quarts antérieurs.

Brun foncé. Front et vertex à pubescence argentée, pronotum orné de quatre grandes taches discales argentées, deux prémédianes et deux postérieures. Sur chaque élytre une large bande longitudinale discale argentée peu nette. Dessous du corps à fine pubescence argentée. Fémurs rouges.

Long.: 13–17 mm.

Type: 1 ♂ du Cameroun: Sanaga, Dibongopflanzung à l'Institut Royal des Sciences Naturelles de Belgique. Allotype: idem.

14. *ruandae* n. sp.

Elancé. Antennes un peu moins longues que le corps, le scape densément et très finement ponctué. Pronotum sensiblement plus long que large, assez densément, mais peu profondément et peu régulièrement ridé en travers. Elytres arrondis à l'apex, densément et très finement ponctués.

Brun foncé. Pronotum avec deux larges bandes longitudinales discales dorées, qui convergent vers l'avant mais n'atteignent ni le bord antérieur ni le bord postérieur. Sur chaque élytre une assez large bande longitudinale dorée légèrement incurvée parcourant les deux tiers antérieurs, courbée en arrière vers le bord latéral, ainsi qu'une assez grande tache circulaire préapicale dorée. Dessous du corps, tibias, tarses et antennes à fine pubescence grise. Sterna revêtus d'une dense pubescence argentée. Fémurs d'un rouge vif.

Long.: 10 mm.

Type: de Ruanda: Shongugu, 1500 m., 6–IV–53, leg. P. Basilewsky, au Musée de Tervueren.

15. *kraatzi* Jord.

Derolus kraatzi Jordan, 1903, Novit. Zool. X, p. 136.

Elancé. Antennes un peu moins longues que le corps, le scape très finement ponctué. Pronotum un peu plus long que large, très faiblement ridé et pourvu d'une dépression postmédiane en fer à cheval peu profonde. Elytres arrondis à l'apex, densément et très finement ponctués sur les trois quarts antérieurs.

Brun rougeâtre foncé, couvert d'une fine pubescence brun grisâtre. Ecusson à pubescence jaune pâle. Sur chaque élytre une très étroite bande transversale prémédiane ondulée jaune et une tache préapicale discale jaunâtre vague. Metépisternes revêtus d'une assez dense pubescence jaunâtre. Pattes et antennes rougeâtres.

Long.: 8 mm ½. Type au Muséum de Paris.

Décrit par Jordan sur un individu du Cameroun: Johann Albrechtshöhe.

16. *arciferus* Gah.

(Fig. 2)

Pachydissus (Derolus) arciferus Gahan, 1891, Ann. Mag. Nat. Hist. (6) VII, pp. 27, 30.

Pachydissus arciferus Kolbe, 1893, Stett. ent. Ztg. LIV, p. 60.

Derolus arciferus Lepesme, 1947, Bull. Soc. ent. Fr. p. 152; 1953, Cat. Col. Ceramb. de Côte d'Ivoire, Pl. VIII, Fig. 2.

Elancé. Antennes un peu plus longues que le corps (♂) ou sensiblement moins longues (♀), le scape finement ponctué et ridé. Pronotum aussi long que large, ridé en travers sur les côtés du disque et pourvu d'une profonde dépression postmédiane en fer à cheval, faiblement ridé en travers sur sa partie médiane antérieure. Elytres arrondis à l'apex (l'angle sutural étiré en une épine minime), densément et finement ponctués sur le quart basilaire, très finement sur le deuxième quart, obsolètement sur la moitié postérieure.

Brun foncé, couvert de pubescence soyeuse grise formant sur les élytres selon la lumière des taches nuageuses.

Long.: 12–18 mm. Type au British Museum.

Décrit par Gahan sur des individus du Sénégal. Côte d'Ivoire: Bouaké. Togo (Kolbe); Niger: D'Akassa à Onitscha, leg. Dr. Cook (Muséum de Paris); Oubanghi: Fort Sibut (idem.); Congo belge: Lulua Kapanga, IX–52, leg. F. G. Oberlaet, Bassin Lukuga, IV–VII–34, leg. De Saeger (Musée de Tervueren), Sandoa, X–30, leg. F. G. Overlaet (idem.).

17. *subaureus* Jord.

Pachydissus (Derolus) subaureus Jordan, 1894, Nov. Zool. I, p. 151.

Assez robuste. Antennes un peu plus longues que le corps (♂) ou sensiblement moins longues (♀), le scape très densément et finement ponctué et ridé. Pronotum un peu plus long que large, profondément ridé en travers dans la moitié postérieure et pourvu de deux petits tubercules prémédians rapprochés de la ligne médiane. Elytres faiblement et assez largement tronqués à l'apex, très densément et obsolètement ponctués.

Brun foncé, couvert d'une pubescence soyeuse dorée formant sur les élytres selon la lumière des taches nuageuses.

Long.: 13–26 mm. Type au Muséum de Paris.

Décrit par Jordan sur un exemplaire d'Abyssinie: Bahr-el-Abiad. Oubanghi: Fort Crampel (Inst. Roy. Inst. Sc. Nat. Belg.); Congo belge: Sandoa, 10–X–30, leg. F. G. Overlaet (Musée de Tervueren); Transvaal: Shilovuvane, leg. H. Junod, Lady Smith, leg. Dr. Martin (Muséum de Paris); Nyasaland: Zomba, 12–XI–43 (Musée de Bulawayo); South Rhodesia: Sabi Valley, XI–43 (idem.).

18. *pseudaureus* n. sp.

Proche de *subaureus* Jord., mais les antennes de moitié plus longues que le corps (♂) ou un peu moins longues (♀), le pronotum peu profondément et irrégulièrement ridé et pourvu d'une dépression postmédiane en fer à cheval, les plus distinctement tronqués à l'apex et un peu moins finement ponctués dans la moitié antérieure.

Type: 1 ♀ du Haut-Sénégal-Niger: Koulouba, leg. J. Vuillet à l'Institut Royal des Sciences Naturelles de Belgique. Allotype du Gabon au Muséum de Paris.

19. *spurius* Jord.

Derolus spurius Jordan, 1903, Nov. Zool. X, p. 137.
Derolus subdilatatus Lepesme et Breuning, 195.

Proche de *subaureus* Jord., mais plus élancé, les antennes d'un tiers plus longues que le corps (♂) ou aussi longues (♀), le scape un peu plus épais, le pronotum très profondément et irrégulièrement ridé et sans tubercules, les élytres plus étroitement tronqués à l'apex, les pattes et les antennes rouges.

Type au Muséum de Paris.

Décrit par Jordan sur des individus du Cameroun: Johann Albrechtshöhe. Doumé, 1930, leg. P. Caral (Muséum de Paris); Congo belge: Sankuru, Kondué, leg. E. Luja (Musée de Tervueren); *subdilatatus* Lep. et Breun. est un synonyme.

20. *malaisei* n. sp.

Elancé. Antennes un peu moins longues que le corps, le scape très densément et finement ponctué. Pronotum un peu plus long que large, densément et profondément, mais irrégulièrement ridé. Elytres arrondis à l'apex, densément et assez finement ponctués, les points très fins dans le tiers apical.

Brun foncé, couvert d'une fine pubescence grise, cette pubescence formant sur les élytres selon la lumière des taches nuageuses. Front, vertex et disque du pronotum parsemés de nombreuses taches dorées.

Long.: 17–23 mm.

Type: 1 ♂ du Tanganyika: Lukuledi, 1905 au Musée de Stockholm; 1 ♀ de même provenance mais en très mauvais état semble appartenir à la même espèce; 1 ♂ de Rhodésie (Musée de New York); South Rhodesia: Sabi Valley, XII–41, leg. D. Townley (Musée de Bulawayo).

21. *sulcatus* Auriv.

Derolus sulcatus Aurivillius, 1928, Ann. Mus. civ. Genova, LII, p. 488.

Elancé. Antennes d'un quart plus longues que le corps (♂) ou aussi longues (♀), le scape éparsément et très finement ponctué. Pronotum un peu plus long que large, profondément et irrégulièrement ridé sur les parties latérales du disque et pourvu d'une dépression postmédiane peu profonde en fer à cheval dont les deux branches latérales sont peu accusées. Elytres arrondis à l'apex, absolètement ponctués.

Brun rougeâtre, couvert de pubescence dorée à forts reflets soyeux.

Long.: 10–16 mm. Type au Musée de Gênes.

Décrit par Aurivillius sur des individus de Somalie: Bas Giuba, Bidi Scionde. Kenya: Taveta, III–12, 750 m., leg. Alluaud et Jeannel (Muséum de Paris), Voi, 600 m. (Inst. Roy. Sc. Nat. Belg.); Tanganyika: Lukuledi (Muséum de Paris); Congo belge: Katanga, Mulando, 10–IX–24, leg. Ch. Seydel (Musée de Tervueren); South Rhodesia: Sabi Valley, X–42, leg. P. Townley (Musée de Bulawayo).

22. *incultus* Gerst.

Cerambyx (Hammaticherus) incultus Gerstaecker, 1855, Monatsber. Berl. Ak. Wiss., p. 265; 1862, Peter's Reise Mossamb. Ins., p. 319, Pl. XIX, Fig. 1.

Pachydissus (Derolus) somalicus Gahan, 1900, Proc. zool. Soc. Lond., p. 32.

Robuste. Antennes un peu plus longues que le corps (♂) ou un peu moins longues (♀), le scape épais, peu densément et peu finement ponctué. Pronotum aussi long que large, densément et assez régulièrement ridé en travers, plus irrégulièrement sur les parties latérales du disque. Elytres relativement larges, subtronqués à l'apex (l'angle sutural étiré en une très petite épine), imponctués. Fémurs pourvus de carènes peu accusées.

Brun foncé, couvert d'une très fine pubescence brun grise.

Long. 17–20 mm. Type au Musée de Berlin.

Décrit par Gerstaecker sur un individu de Mossambique: Sena; *somalicus* Gah. est un synonyme. Somalie: Dolo (Gahan).

v. *rufoscapus* Auriv. (*Derolus incultus* Gerst. v. *rufoscapus* Aurivillius, 1908, Sjöstedt, Erg. Exped. Kilimandj. VII, p. 143). Comme la forme typique mais le scape et les pattes rouges.

Tanganyika: Meru-Niederung (Aurivillius); Kenya: Athi River, IV–99, leg. Legros, (Muséum de Paris).

23. *brunneipennis* Gah.

Derolus brunneipennis Gahan, 1904, Ins. Transvaal, p. 113, Pl. X, Fig. 5.

Elancé. Antennes d'un quart plus longues que le corps (♂) ou sensiblement moins longues (♀), le scape très densément et finement ponctué. Pronotum aussi long que large, le disque très faiblement et irrégulièrement ridé et pourvu d'une dépression postmédiane en fer à cheval. Elytres subtronqués à l'apex, obsolètement ponctués sur les trois quarts antérieurs.

Brun foncé, couvert d'une fine pubescence brun grisâtre. Antennes rougeâtres.

Long.: 12–17 mm. Type au British Museum.

Décrit par Gahan sur des exemplaires de Transvaal: Waterberg District. Pretoria, 27–X–45, leg. G. van Son; South Rhodesia: Sawmills, 16–XI–22, leg. Neville Jones (coll. Tippmann); South Rhodesia: Bindura, I–47, leg. Rev. Smith (coll. Hunt); Damaraland: Okahandja (coll. Tippmann); Zambezi: Barotse Country, VIII–96 (Muséum de Paris); Swaziland: Bremmetsdorp, XII–51, leg. O. Mennie (coll. Hunt); Abyssinie: Dire Daua, Hora Dun (coll. Lepesme); Somalie: Bardera, II–93, leg. E. Ruspoli (Musée de Gênes); Giuba: Margherita, IV–20, leg. Patrizi (idem).

24. *martini* n. sp.

Robuste. Antennes aussi longues que le corps, le scape très densément et assez grossièrement ponctué et ridé. Pronotum aussi long que large, densément, profondément et régulièrement ridé en travers. Elytres légèrement tronqués à l'apex (l'angle marginal bien apparent), extrêmement densément et peu finement ponctués sur le quart basilaire, très finement ponctués sur le restant de leur surface.

Brun foncé, couvert d'une très fine pubescence brun grisâtre. Long.: 15 mm.

Type: ♀ de Djibouti, leg. Dr. Martin au Muséum de Paris.

25. *bifarius* Duffy

Derolus bifarius Duffy, 1953, Ruwenzori Exped., III, no. 12, p. 165, Figs. 1,2.

Elancé. Antennes ne dépassant pas le milieu des élytres, le scape éparsément et finement ponctué, les articles trois et quatre faiblement grossis à l'apex. Pronotum aussi long que large, pourvu dans la moitié antérieure de deux rides circulaires et dans la moitié postérieure de trois rides transversaux. Elytres faiblement tronqués à l'apex (l'angle sutural étiré en une petite épine), densément et très finement ponctués.

Brun foncé, le quart apical des élytres brun clair. Pattes jaunâtres, le tiers apical des fémurs, la base et l'apex des tibias, brun noir. Tarses brun foncé. Antennes à fine pubescence grise. Dessus du corps probablement frotté.

Long.: 18 mm. Type au British Museum.

Décrit par Duffy sur un exemplaire (♀) d'Uganda: Bukundo, Bwamba Pass.

26. *mauritanicus* Buq.[1]

Hammaticherus mauritanicus Buquet, 1840, Ann. Soc. ent. Fr., IX, p. 295.
Hammaticherus nerii Erichson, 1841, Wagner Reise, III, p. 188, pl. VIII, Fig. 11.
Cerambyx nerii Mulsant, 1862, Col. Fr. Long., ed. 2, p. 58.
Derolus mauritanicus Lepesme, 1947, Bull. Soc. ent. Fr., p. 152.
Derolus mauritanicus Villiers, 1946, Fna. de l'Emp. franc., V, Col. Ceramb. Afr. Nord, p. 80, Fig. 185.

Elancé. Antennes d'un quart plus longues que le corps (♂) ou beaucoup moins longues (♀), le scape densément et finement ponctué et ridé. Pronotum un peu plus long que large, rétréci vers l'avant, profondément ridé en travers. Elytres subtronqués à l'apex l'angle sutural étiré en une très petite épine), extrêmement densément et obsolètement ponctués.

Brun rougeâtre à brun foncé, les pattes et les antennes rouges, couvert d'une fine pubescence soyeuse brun grise.

Long.: 15–22 mm.

Décrit par Buquet sur des individus d'Alger; *nerri* Er. est un synonyme.

Maroc, Algérie, Tunisie (Villiers).

27. *parus* Jord.

Derolus parus Jordan, 1903, Novit. Zool. X, p. 137.

Elancé. Antennes d'un tiers plus longues que le corps (♂) ou un peu plus longues (♀), le scape très court, très densément et peu finement ponctué. Pronotum beaucoup plus long que large, densément et profondément mais très irrégulièrement ridé. Elytres arrondis à l'apex, densément et très finement ponctués sur les trois quarts antérieurs.

Brun rougeâtre, couvert d'une fine pubescence soyeuse brun grise. Pronotum orné de taches dorées.

Long.: 9 mm. ½—17 mm. Type au Muséum de Paris.

Décrit par Jordan sur des individus de Guinée espagnole: Benito; Congo belge: Lukolela, 1937, leg. R. Massart; Cameroun: Mundame, Sanaga (Inst. Roy. Sc. Nat. Belg.); Cameroun: Victoria; Ja River, XII–05–IV–06 (Muséum de Paris); Ubanghi: Libenge, 8–II–36, leg. C. Léontowitch (Musée de Tervueren); South Rhodesia: Sabi Valley, XI–43, leg. P. Townley (Musée de Bulawayo).

Ssp. *punctipennis* nova: Comme la forme typique, mais plus grand, les élytres ponctués moins finement.

Long.: 20 mm.

Type: 1 ♀ de Guinée francaise: Mt. Nimba, 28–III–55, leg. J. G. Pointel dans la collection Lepesme.

2. SG. *SPINIDEROLUS* NOVA

Troisième article des antennes étiré en une épine apicale interne, le quatrième article beaucoup moins long que le cinquième, le pronotum ridé, les fémurs claviformes.

Type: *euparus* Auriv.

28. *euparus* Auriv.

Pachydissus euparus Aurivillius, 1907, Ark. f. Zool., III/18, p. 6.

Elancé. Antennes presque deux fois plus longues que le corps (♂) ou d'un quart plus longues (♀), le scape très densément et assez grossièrement ponctué et ridé, le troisième article étiré à l'angle apical interne en une épine, cette épine plus longue chez le mâle. Pronotum beaucoup plus long que large, densement, profondément et très irrégulièrement ridé. Elytres arrondis à l'apex, densément et très finement ponctués sur les trois quarts antérieurs.

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[1] Cette espèce est répandue vers l'est jusq'en Asie occidentale en y formant une sous-espèce distincte: sbsp. *iranensis* nov. *Iranenis* differt de la forme typique par le disque du pronotum plus faiblement ridé et la ponctuation élytrale très fine mais pourtant beaucoup plus distincte.

Type: d'Iran: Makran, Sud-est de Nahu, 1300 m., 29 et 26-III-54, leg. Richter et Schäuffele au Musée de Stuttgat. Quatre paratypes de même provenance, ou de Belutschistan, Iranshar, 800 m., 11-18-III-54, leg. Richter 5 Schäuffele au Musée de Stuttgat et dans la coll. Lepesme.

Brun foncé, couvert d'une fine pubescence soyeuse brun grise. Pronotum orné de taches dorées.

Long.: 12–27 mm.

Décrit par Aurivillius sur un individu du Cameroun.—Côte d'Ivoire: Abengourou, 26–II–51, dans la collection Lepesme. Guinee française: Mt. Nimba, 28–III–55, leg. J. G. Pointel (idem.); Cameroun: Buea (Muséum de Paris); Congo belge: Kasai, 1904, leg. Edm. Taymans (Muséum de Paris); Mayumbe, 1917, leg. R. Mayné. Congo da Lemba, X–11, leg. R. Mayné, Eala, Boyeka 1915, leg. R. Mayné (Musée de Tervueren); Angola: Hrambo, 1934, leg. J. Piementel (idem.); Tanganyika: Lindi, 1–XI–03 (Inst. Roy. Sc. Nat. Belg.).

3. SG. *GRACILIDEROLUS* NOVA

Troisième article des antennes non étiré en une épine apicale, le quatrième article beaucoup moins long que le cinquième; disque du pronotum ridé; fémurs postérieurs pédonculés.

Type: *gracilis* Lep. et Breun.

29. *gracilis* (Auriv. i. l.) n. sp.

Très élancé. Antennes un peu moins longues que le corps, le scape très finement ponctué. Lobes supérieurs des yeux se touchant presque. Pronotum beaucoup plus long que large, pourvu de quelques rides transversaux sur sa partie médiane. Elytres très longs et étroits, arrondis à l'apex, très densément et finement ponctués sur toute leur étendue. Fémurs postérieurs pédonculés.

Brun rougeâtre, couvert d'une fine pubescence gris blanchâtre. Disque du pronotum ainsi qu'une grande tache triangulaire postscutellaire sur les élytres revêtus de pubescence brun jaunâtre. Elytres avec quelques très étroites bandes longitudinales brun rougeâtre qui s'élargissent facilement dans la partie préapicale de l'élytre et se joignent partiellement. Moitié basilaire des fémurs, les tibias et les antennes rouges à fine pubescence gris blanchâtre.

Long.: 12 mm.

Type: de South Rhodesia: Bulawayo au Musée de Stockholm; South Rhodesia: Sabi Valley, 26–X–45, leg. P. Townley (Musée de Bulawayo).

4. SG. *DISSAPORUS* AURIV.

Dissaporus Aurivillius, 1907, Ark. f. Zool., III/18, p. 8.

Aporus Fahroeus, 1872, Öfvers. Vet. Ak. Förh. XXIX/1, p. 54.

Troisième article des antennes non étiré en une épine, le quatrième article un peu moins long que le cinquième; disque du pronotum densément ponctué mais non ridé; fémurs postérieurs claviformes.

Type: *cylindricus* Fahr.

30. *cylindricus* Fahr.

Aporus cylindricus Fahroeus, 1872, Öfvers. Vet. Ak. Förh. XXIX/1, p. 54.

Pachydissus pauper Gahan, 1904, Distant, Ins. Transvaal., p. 113, pl. X, fig. 8.

Elancé. Antennes sensiblement moins longues que le corps, le troisième article de moitié plus long que le quatrième, sensiblement plus long que le cinquième. Pronotum beaucoup plus long que large, très densément et assez finement ponctué. Elytres étroitement subtronqués à l'apex, très densément et peu finement ponctués sur toute leur étendue.

Rouge, couvert de pubescence jaune paille, tout le dessus marbré de brun rougeâtre.

Long.: 13 mm.

Décrit par Fahroeus sur des individus de Caffrérie.—Loewfontain, North Transvaal, 4–XII–50 dans la collection Lepesme; Congo belge; Elisabethville. X–24, leg. Ch. Seydel au Musée de Tervueren; Tanganyika: Tununguo, ex coll. Clermont (Musée de Tervueren); Zambezi: Chemba, X–35, leg. J. Surcouf (Muséum de Paris). *Pauper* Gahan est un synonyme.

31. *cachani* n. sp.

Proche de *puncticollis* Lep. et Breun., mais le pronotum encore plus long, très finement ponctué, les élytres plus grossièrement ponctués, chacun avec une carène longitudinale discale faiblement ondulée et très peu accusée.

Type: 1 ♀ de Côte d'Ivoire: Adiopodoumé, 11-IV-53, leg. P. Cachan, dans la coll. Lepesme; 1 paratype de même provenance, 13-III-53.

32. *mythicus* Gyll.

Stenochorus mythicus Gyllenhal, 1817, Schönherr, Syn. Ins., I/3, Append. p. 181.

Proche de *puncticollis* Lep. et Breun., mais les antennes n'atteignant même pas le milieu des élytres, le pronotum assez grossièrement ponctué, les élytres grossièrement ponctués et pourvus, chacun, d'une fine carène longitudinale discale bien accusée, partant de l'épaule et se rapprochant au tiers apical de la suture.

Décrit par Gyllenhal sur des individus de Sierra Leone.—Congo belge: Dima, 15 IX-08, leg. A. Koller au Musée de Tervueren; Haut Sénégal-Niger: Koulouba, leg. L. Vuillet (Muséum de Paris).

5. SG. *MICRODEROLUS* AURIV.

Microderolus Aurivillius, 1925, Rev. Zool. bot. Afric., XIII, p. 52.

Troisième article des antennes non étiré en une épine, le quatrième article un peu moins long que le cinquième; disque du pronotum lisse, ni ponctué ni ridé; fémurs postérieurs claviformes.

Type: *latevittatus* Auriv.

33. *latevittatus* Auriv.

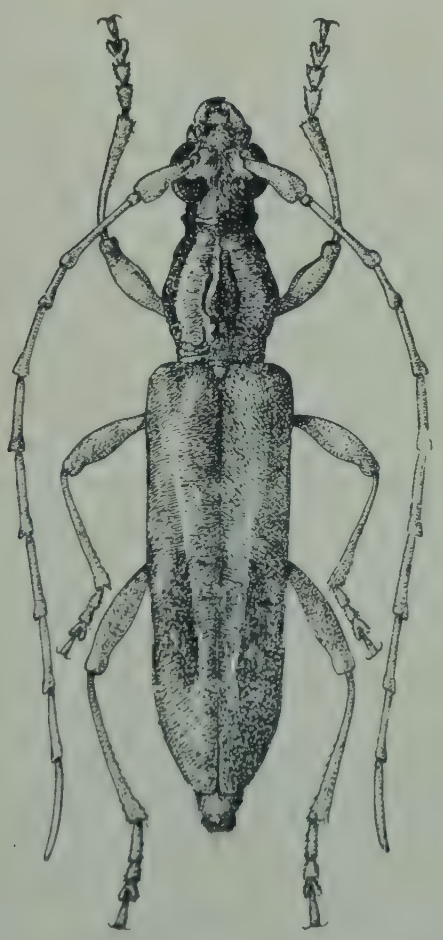
Microderolus latevittatus Aurivillius, 1925, Rev. zool. bot. Afric., XXII, p. 53, Fig.

Elancé. Antennes beaucoup moins longues que le corps, le troisième article beaucoup plus long que le quatrième, nettement plus long que le cinquième. Pronotum beaucoup plus long que large, lisse. Elytres arrondis à l'apex, très densément et très finement ponctués et pourvus, chacun, de deux faibles crêtes longitudinales discales, dont l'interne est obtuse et s'efface au milieu de la longueur de l'élytre et dont l'externe, sublatérale est plus nette et s'étend presque jusqu'à l'apex.

Noir, l'écusson, les élytres, le dessous du corps, les pattes et les articles antennaires à partir du cinquième couverts d'une fine pubescence argentée. Sur chaque élytre deux larges bandes longitudinales discales allant de la base jusqu'à un peu au delà du milieu leur longueur, blanches à leurs parties basales et apicales, d'un brun rougeâtre clair sur le de reste de leur parcours.

Long.: 9 mm.

Décrit par Aurivillius sur un exemplaire du Congo belge: Lueba (Musée de Tervueren).



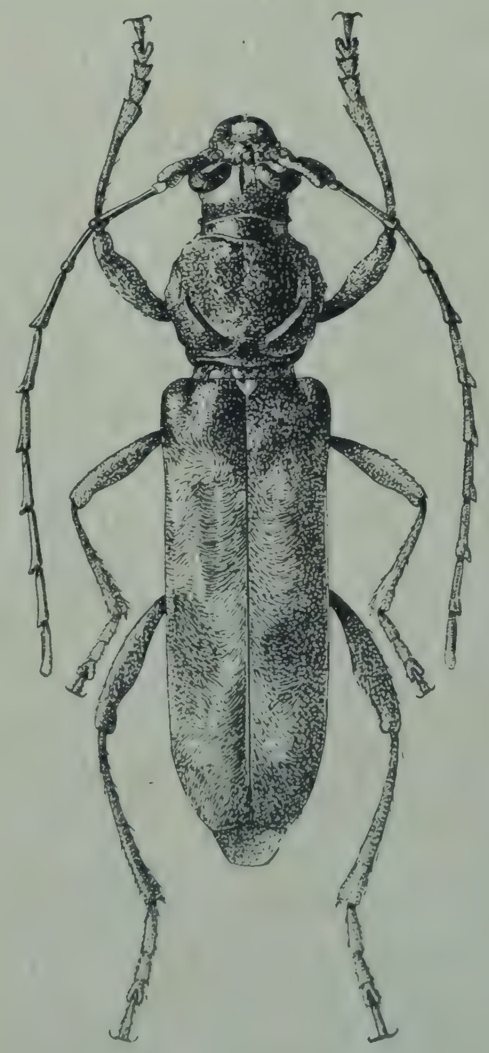


Fig. 1 (gauche). *Derolus dilatatus* Chevr. Fig. 2 (droite). *D. arciferus* Gahan.

Breeding Habits of Arboricole Insects in Central Africa

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ABSTRACT

The tropical rain forests are inhabited by a number and variety of tree infesting insects not found in other forest types. With few exceptions, we find there species of the same systematic units as in the Palaearctic and Neartic Regions, and additionally some other groups. The variety of breeding habits is much larger than elsewhere, not only in general, but also within each of the larger groups living under the bark or in the wood of the trees. There also exist intermediate links between the rather fixed breeding types found in the Holarctic Region. True xylophagia is common in the Bostrychidae, Anobiidae, Cerambycidae, Buprestidae, Cossonidae, and Curculionidae, and is also observed in certain Scolytidae. Phloeophagia, probably the second step in the phylogeny of breeding habits of arboricole insects, is typical of a great number of Scolytidae and of some Curculionidae, Buprestidae, and Cerambycidae. These two types of breeding habits are connected with each other by some species of Scolytidae and Bostrychidae, in which larval development begins as true phloeophagia, switching in the later larval stages into xylophagia. The third and most specialized breeding habit is xylo-mycetophagia, in which the larvae do not feed on the wood but on the mycelia of ambrosia fungi cultivated on the walls of the breeding tunnels. Such xylo-mycetophagia is found in all Platypodidae, in certain groups of Scolytidae, in the Lymexylonidae, and in a number of Brenthidae and Curculionidae.

Fours years ago, in 1952, The Institut National pour l'Etude Agronomique du Congo Belge invited the author to come to the Belgian Congo to make there a survey of the wood infesting insects, especially of the superfamily Scolytoidaea, including their biology and ecology. Although the time available for such a huge program was very short, altogether six months, it was possible to gather quite a large number of observations, a small part of it being the base for the following statements.

FEEDING HABITS

Tree infesting insects generally are divided into various groups according to the feeding habits of the immature stages, their adaptation to their foodplants, and to the state of health of the trees attacked.

As far as the feeding habits of the larvae are concerned we distinguish:

Phyllophagy (feeding upon the leaf tissue).

Phloeophagy (feeding upon the living tissue under the bark).

Cortiphagy (feeding upon the outer dead layers of the bark).

Xylophagy (living in the wood and getting the nutrition with the aid of entosymbiontes located either in certain cells or groups of cells, so-called mycetoms, along the digestive channel (intracellular entosymbiosis) or floating freely in the intestines (extracellular entosymbiosis).

Xylo-mycetophagy (a new term proposed to be used for larvae not feeding on the wood itself but upon the mycelium of fungi cultivated on the walls of their tunnels).

Aside from these major groups, one often distinguishes species living within the stems of herbaceous plants and species breeding in fruits and seeds. The latter are of no interest within the scope of this paper, and the same is true of the phyllophagous species. Cortiphagous insects seem to be very rare in the tropical forests, at least in the African rain forests and have not been observed as yet.

Herbiphagy

This is rather common to a good number of Coleoptera, like many Cerambycidae and Curculionidae, some Lepidoptera, Hymenoptera, and Diptera. Within the Scolytidae, herbiphagy is rare but can be found in a few Hylesinae and Ipinae. Well known examples have been recorded in *Hylastinus obscurus* Marsh., a beetle breeding in the stems and roots of leguminous plants such as *Trifolium*, Alfalfa, *Medicago*, etc., in the Palaearctic

Region and also in the Nearctic, in various species of *Thamnurgus* Eichh. (Crypturgini) in the southern parts of Europe, Transcaucasia, and Africa living in the stems of Ranunculaceae (*Aconitum*, *Delphinium*), Labiatae (*Teucrium*, *Origanum*, *Lamium*, *Betonica*) and various species of *Euphorbia*. Other species of similar breeding habits are found in the genera *Liparthrum* Woll., *Aphanarthrum* Woll., and *Xylocleptes* Ferr. In Central Africa there also exist some species of *Lanurgus* Egg. (Micracini), which make larval tunnels in stems of herbaceous plants.

PHLOEOPHAGY

Phloeophagy is most widely distributed in the family Scolytidae, a fact familiar to all forest entomologists.

The subfamily Scolytinae, distributed over the entire Holarctic and the Neotropical Region comprises species exclusively living under the bark of twigs, branches, and trunks of trees and shrubs. Complementary feeding of the young immature beetles sometimes takes place in small twigs or in buds.

Concerning the subfamily Hylesinae, our knowledge of breeding habits is based largely on observations made in the Palaearctic and Nearctic regions, to a lesser extent on such in Indomalaya, and according to these phloeophagy was thought to be the only type of feeding for the developing larvae. In the meantime the African Hylesinae have been studied to a certain extent, bringing to light some new very interesting facts. According to these, phloeophagy is not the only way by which Hylesinae may obtain their food during larval development, although the greater part of this subfamily lives between the bark and the sapwood in the living tissue of trees and shrubs. As far as Africa is concerned, phloeophagous Hylesinae are common in all forest types.

The subfamily Xyloctoninae, endemic to Africa and the Indomalayan region, also lives exclusively phloeophagous. The two African genera of the Xyloctoninae, *Xyloctonus* Eichh. and *Ctonoxylon* Hag. are rather common in the tropical rain forest and have been reported from other forest types in the east from Abyssinia to South Africa.

The breeding habits of the subfamily Ipinae are much less uniform. Of the tribes belonging to it, the Ipini, Crypturgini (with the exception of the spermatophagous *Coccotrypes* Eichh. and *Poecilips* Schauf.), Pityophthorini, Cryphalini and Micracini largely live under the bark, some genera exclusively so, while in others exceptions are more or less common. The Corthylini and the Xyleborini, like the species of the Scolytoplatypodinae, never breed phloeophagously.

All truly phloeophagous insects attack their hosts either in a perfectly healthy stage or as secondary enemies of trees, i.e., after they have been damaged by some other cause or after they have been felled. They are common in windthrown trees or broken branches, in fire-swept forests, in stands where the level of ground water has been changed, etc. Many phloeophagous species ordinarily secondary in their attack may become primary enemies after the density of population has reached a certain level.

The nutritive value of the breeding material available to phloeophagous insects in the cambium of the bark certainly is very high, and this fact may explain why the Scolytidae are regarded as some of the most dangerous forest insects in the Holarctic Region. Nutrition being at an optimum, it only depends on the abiotic environment conditions to shorten the time of development, to increase the number of generations per season, and consequently to produce infestations of all grades of intensity.

Probably connected with this high value of nutritive material is the fact that, as far as Africa is concerned, trees producing latex in some form usually are much more commonly and more heavily attacked by phloeophagous Scolytidae than plants without such excretions. Analogous with this fact, we notice a distinct preference of coniferous trees producing resin of some kind against non-resinous and non-latexous broadleaved trees in the Palaearctic and Nearctic Regions. The only exception for Africa so far observed is the well known *Hevea brasiliensis* Müll. Arg., which never was attacked by phloeophagous Scolytidae, while xylo-mycetophagous insects are rather common. If this observation also holds true for the native countries of *Hevea*, in the Neotropical Region, we were not in the position to find out.

Another peculiarity of tropical phloeophagous Scolytidae in Africa seems to be that they attack trap trees or windthrown timber more early than species with other, we may say xylophagous or xylo-mycetophagous, breeding habits. In a number of cases the latter entered the wood while the former already had developed to nearly fully grown larvae or pupae.

Of other Coleoptera living phloeophagously in Central Africa, there might be mentioned certain Curculionidae breeding like *Pissodes* in the Holarctic Region and some Buprestidae and Cerambycidae. A few Bostrychidae and Cossonidae feed phloeophagously in their early larval stages, while later on they enter the wood, continuing their development in a truly xylophagous manner.

Closing this chapter, it may be mentioned that the greater part of trees in the African forests are not attacked by phloeophagous insects, leaving there an ecological vacuum not made use of as yet by insects.

XYLOPHAGY

With the concept of xylophagy, we usually connect the feeding habits of the Bostrychidae, Anobiidae, Cossonidae, many Cerambycidae, Buprestidae, some Curculionidae, horntails or wood wasps, and certain Lepidoptera like the Cossidae and Sesidae.

Xylophagous insects usually attack their hosts after the trees or parts of them have died for some reason; the cells of the wood may contain living plasma or not. Therefore xylophagous insects are regarded as secondary, as necrophytophagous or as saprophagous. In all cases observed up to date, these xylophagous insects never digest cellulose or lignin directly, but always with the aid of microorganisms, entosymbionts which decompose the wood particles already in the digestive channel by producing cellulase.

An intracellular entosymbiosis (the microorganisms living in cells of the digestive channel or in specialized groups of cells, so called mycetoms) is found in species or groups of species attacking rather healthy wood either in the forest itself or already used in buildings or furnitures. The other type of entosymbiosis, the extracellular, where the microorganisms float freely in the digesting channel or in special extensions of it, the so-called fermenting chambers, are more typical for species living in detoriating or largely decomposed wood.

Most xylophagous insects digest only a small portion of the material actually fed upon and therefore the galleries of such species ordinarily are packed with excrements of the larvae, the so-called "Bohrmehl" in German.

Within the Scolytidae, xylophagy has not been reported yet, but all species were regarded as phloeophagous or xylo-mycetophagous. In Central Africa recently, some very striking examples of xylophagous species with breeding habits rather similar to those of many Cossonidae, Bostrychidae, and certain Curculionidae have been observed. Such xylophagous Scolytidae belong to genera ordinarily phloeophagous and seem to represent exceptions to the general rule.

In the Palaearctic Region it is well known that certain species like *Leperisinus fraxini* Ratz. and *Blastophagus minor* Hartig live under the bark during the larval stage but sometimes enter the wood at the end of their development to construct their short cup-like pupal chambers. The breeding habits of the African Scolytidae feeding on wood itself are quite different, and we also find intermediate forms in which, during a part of their development, the larva live like phloeophagous insects, while in the second half of their life they enter the wood itself, feeding there like truly xylophagous species, as the Cossonidae or Bostrychidae.

Other, more specialized, species live entirely in the wood, the adult beetles as well as the larvae.

Naturally it is quite difficult to draw any conclusions on the phylogeny of the xylophagous feeding habits, whether they should be regarded as a high grade of specialization or an early stage of development. At the present time, in comparison with other xylophagous insects and regarding the grade of decomposition of the breeding material of such species, the latter conclusion, that we have to deal with an early stage of development, becomes more convincing than a high grade of specialization adopted later on.

Xylophagy in the Scolytidae has been found in Africa among several genera of the subfamily Hylesinae, in *Strombophorus ericius* Schauf., *Rhopalopselion grandis* Schedl, and *Rhopalopselion intermedium* Schedl. Within the Ipinae we found true xylophagy in two species of *Mimips* (*arundinarius* Schedl, *kikusuae* Schedl) of the tribe Ipini and in *Micracidendron montanum* Schedl of the Micracini.

Of the Anthribidae observed in forest trees in Africa, some feed in their larval stage like other true xylophagous insects while others, like *Gulamentus pardalis* Jordan, have their galleries in the first part of their development under the bark, later on in the wood. Similar feeding habits are also found in some Bostrychidae in which a change from phloeophagy to xylophagy may occur during the larval stage under certain conditions. Examples of that type have been observed in *Xyloperthodes nitidipennis* Murray and *Xylopertha piceae* Oliv., in both cases in freshly dying trees. Probably the content of moisture of the trees attacked has something to do with this change of feeding habits. All Cossonidae so far observed in Central Africa live exclusively xylophagously, while the feeding habits of the Buprestidae and Cerambycidae usually do not differ to any extent from those of Holarctic species, except some spermatophagous species which are of no interest within the scope of this paper.

XYLO–MYCETOPHAGY

The highest grade of specialization in wood inhabiting insects is reached when the larva do not feed on the wood itself, but use for their nutrition the mycelium of certain fungi, the so-called ambrosia fungi, cultivated on the walls of the galleries made by the parent beetles. To distinguish this type of ectosymbiosis from others, for instance that of certain white ants, we suggest using the combination "xylo-mycetophagy" for all ambrosia-feeding insects. The symbiosis with such fungi certainly enables the larvae to grow rather quickly on the highly concentrated food rich in proteins. These fungi can be cultivated by insects in a very great number of trees in the tropical rain forests, to a lesser extent in such of the temperate zones. Therefore xylo-mycetophagy is very common around the equator, becoming more and more scarce towards the colder climates, contrary to the distribution of the phloeophagy already discussed.

Xylo-mycetophagy within the Scolytidae is restricted to two tribes of the subfamily Ipinae, which are the Corthylini and the Xyleborini, and within these groups there do not exist any exceptions. Other units exclusively xylo-mycetophagous are the subfamily Scolytoplatypodinae and the family Platypodidae. Outside the superfamily Scolytoidea, xylo-mycetophagy is rare, but we find it realized in certain Lymexylonidae, the genera *Scolytoproctus* and *Gulamentus* of the Curculionidae and in the Calodromini and Taphroderini of the Brenthidae.

The physiological conditions of the breeding material in the xylo-mycetophagous insects vary within rather narrow limits. Such insects never breed in dry or decaying wood but always in freshly felled trees or in recently windthrown timber or branches, facts which certainly are narrowly connected with the growth of fungi in the galleries. This stage of physiological condition usually does not last very long during the summer in the Holarctic Region, except when lumber is piled in very moist places like in narrow valleys or along rivers and lakes. The same observations could be made in the dry forest of Africa and on larger clear cuts in the rain forest. Much longer time seems available for successful breeding, if the trees are felled singly in rain forest or when lumber is stored in narrow lines in dense forests.

HOST SELECTION

During the carboniferous period, we have no proofs that land inhabiting plants were attacked by wood-breeding insects. This is supported by two facts; we have not found any galleries in Carboniferous plants, and the insect fauna of this epoch generally is classified as omnivorous or detritovorous. A third proof may be the absence of wood-inhabiting insects in the Pterydophytae of today, as represented in the tree like ferns of tropical countries.

The beginning of specialization in the way of nutrition may have occurred in the Triassic during the appearance of the first holometabolous insects and may have found its greatest expansion during the Cretaceous period, with the appearance of the first angiosperms. How far another branch of plants, the coniferous trees of the Permian period, has influenced this development is quite difficult to judge at present. In the older parts of the Tertiary formation we find all main types of wood-inhabiting insects of our day represented by rather modern morphological aspects, like the Bostrychidae, Anobiidae, Lyctidae, Lymexylonidae, Cerambycidae, Curculionidae, Lucanidae, and Scolytidae, while some Buprestidae have been observed in somewhat older layers of the Triassic formation.

While, for these rather old fossils, our conclusions about their breeding habits can only be based on the analogy of morphological aspects, we may draw such with more probability with regard to the fauna of the baltic amber. The greatest part of amber Scolytidae is most closely allied to recent species living in coniferous trees, and, as the amber forest consisted to a large extent of conifers and the chances of getting entangled in the resin of these trees are much greater than in broadleaved trees, we may taken it for granted that the majority of amber Scolytidae actually bred in trees of the genera *Pinus*, *Sciadopitys*, *Sequoia*, *Juniperus*, *Thuja*, *Libocedrus*, *Cupressus*, and *Taxodium*. For a few other species closely allied to broadleaf-inhabiting forms of today, we can draw similar conclusions. By far the greatest part of the fossil Scolytidae found so far belongs to recent groups or genera living exclusively phloeophagously. Xylo-mycetophagous species are not among those of the baltic amber, or which have been reported from older periods.

In the question of host selection, we usually distinguish between the latter in a normal environment (euphagy) and that under changed circumstances where the insect is forced to make use of some other less suitable hosts in order to survive (xenophagy). Aside from this host selection in a botanical sense, we also find a specialization in insects with regard to certain parts of the plants or trees, some species preferring to breed in small twigs, others in branches, in the trunks or roots. This type of specialization may be very marked so that the species in question can only breed in their preferred host material, or the breeding habits may vary according to the abundance of hosts. This plasticity in the breeding habits of scolytid beetles is rather marked in the untouched African rain forests, but the beetles show a distinct preference concerning the parts of trees attacked as soon as breeding material is increased by cuttings or by the cultivating of forest trees or shrubs on a large scale. In the temperate zones we also know of cases where phloeophagous scolytids change their main host or hosts when the species are distributed over very large areas, and we may expect similar conditions also for the African continent. *Ips concinnus* Mannh., known from Guatemala and along the coast northwards to Alaska, breeds in the southern parts of its distribution in various species of pines; in the north it prefers *Picea sitchensis*. *Pityophthorus nitidulus* Mannh., also a pine insect in the south, breeds in certain species of spruce and balsam in the north.

A strict *monophagy*, which means the selection of a single species of host plant, is rather rare in phloeophagous Scolytidae, and we find examples more commonly in the temperate zones, where a certain host species sometimes covers very large areas without any relatives nearby, than in subtropical and tropical countries. Perhaps we can explain this rather interesting fact by the assumption that the temperate regions represent refuges of a formerly richer fauna and flora in a more favourable climate. During the course of changes in the environment, many insects were forced to specialize towards certain hosts in order to survive. Such examples may be found within the Scolytidae in every one of the large subfamilies. Of the genus *Scolytus* Geoffr., ordinarily breeding in broadleaved trees, we find *Scolytus opacus* Blackm. now restricted to *Abies lasiocarpa* (Hook) Nutt. and *Scolytus laricis* Blackm. to *Larix occidentalis* Nutt. in western United States. The hylesinids *Phthorophloeus spinulosus* Rey and *Xylechinus pilosus* Ratz. ordinarily breed in spruce in the Palaearctic Region, *Pseudohylesinus sitchensis* Sw. in *Picea sitchensis* (Bong.) Karst in British Columbia, Washington, Oregon, and Califonia. In the subfamily Ipinae monophagy occurs in many species of *Ips* Deg., *Pityophthorus* Eichh., in *Xylocleptes bispinus* Duft. (*Clematis vitalba* L.), in *Cryphalus intermedius* Ferr. (*Larix decidua* Mill.), in certain species of *Thamnurgus* Eichh., etc.

Within the scolytid fauna of Africa, monophagy seems to be more rare in the tropical rain forests, with its optimum of abiotic environment conditions, than on its borders where changed humidity and temperature produce forest types of a highly specialized form. In the eastern mountains of the Belgian Congo, the bamboo *Arundinaria alpina* K. Schum. (Graminae) covers very large sites at certain altitudes, and here we have found *Mimips arundinarius* Schedl breeding in this host plant only. Another example of that kind may be *Micracidendron montanum* Schedl in *Alchornea hirtella* Benth. and *Mimips jasminiae* Schedl in *Jasminium abyssinicum* R. Br. In the low lands of the cuvette of the Belgian Congo, three species of *Chortastus*, *agnatus* Egg., *camerunus* Schauf., and *medius* Egg., have so far been observed only on *Staudtia stipitata* Warb. and *Chortastus similis* Egg. only on *Musanga cecropioides* R. Br. *Mimips angylocalyx* Schedl seems restricted to *Angylocalyx Pynaertii* De Wild. and *Pityophthorus pentaclethrae* Schedl to *Pentaclethra macrophylla* Benth., but for all these species records are available for the Belgian Congo only, and monophagy may fall as soon as more detailed investigations are made in other parts of the tropical rain forests. All the monophagous species mentioned are phloeophagous except the first two, *Mimips arundinarius* Schedl and *Micracidendron montanum* Schedl, which may be regarded as truly xylophagous. Further representatives of a rather strict monophagy eventually may be detected in the genera *Hapalogenius* Hag., *Kissophagus* Chap., *Rhopalopselion* Hag., *Metahylesinus* Egg. (Hylesininae), and within the Ipinae in the genera *Thamnurgus* Eichh., and in certain Cryphalini.

Monophagy of the Second Degree

Monophagy, host selection within one and the same botanical genus, is more common than restriction to a single food-plant in the Holarctic Region as well as in the tropics. This type of host preference also might be accomplished if we introduce a second or third tree host species of the same genus into countries where only a single species occurs naturally.

Examples of monophagy of this type may be found in the subfamilies Scolytinae, the Hylesininae (*Pseudohylesinus* Sw., *Scierus* Lec., *Phloeosinus* Chap., *Blastophagus* Eichh., *Carphoborus* Eichh.), the Cryphalini (*Trypophloeus* Fairm., *Ernoperus* Thoms., *Cryphalus* Er.), the Crypturgini (*Dryocoetes* Eichh., *Thamnurgus* Eichh.), and the Ipinae (*Pityophthorus* Eichh., *Pityogenes* Bedel, *Ips* Deg., *Orthotomicus* Ferr., etc).

For the African region we may regard as monophagous in this sense *Strombophorus lukengae* Schedl, breeding on *Dialium Corbisieri* Staner and *Dialium yambataense* Vermoesen, *Cryphalomorphus pleiocarpae* Schedl in *Pleiocarpa micrantha* Stapf and *Pleiocarpa tubicina* Stapf, *Pityophthorus togonus* Egg. in *Carapa grandiflora* Sprague and *Carapa procera* DC., and also in some species of the genus *Thamnurgus* Eichh. in the East African mountain forests. A more convincing account on this subjects needs naturally further and more widespread observations.

All species of the enlarged monophagy breed phloeophagous under the bark.

Oliphagy

Within the concept of oliphagy, we ordinarily distinguish between systematic oliphagy, meaning that a certain species breeds in plants more closely allied such as in a single botanical family (oliphagy first grade) or that the hosts belong to different botanical families of a single order (second grade), or to families of even different orders (third grade). A disjunctive oliphagy occurs when the number of hosts remains restricted but belong to units widely distributed in the botanical system.

In the Holarctic Region phloeophagous Scolytidae are partly restricted to host-plants of the Pinaceae (*Hylastes* Er., *Hylurgops* Lec., *Pseudohylesinus* Sw., *Pityogenes* Bedel, and *Ips* Deg.) and partly to the Cupressaceae (*Phloeosinus* Chap.) within certain geographical regions. In the angiosperms an oliphagy of the first grade is more rare, but we find it realized in some species of the genera *Hylesinus* Fab. and *Leperisinus* Reitt., which breed in certain regions exclusively in Oleaceae.

Within the xylo-mycetophagous Scolytidae also, some striking examples of oliphagy have been observed. A strict oliphagy of the first grade is realized in *Xyleborus eurygraphus* Ratz. in the Palaearctic Region and in *Platypus wilsoni* Sw. in the Nearctic, such of the second grade in *Trypodendron lineatum* Oliv. in the Holarctic Region.

As far as Africa is concerned it is much more difficult to proove a systematic first grade oliphagy. Perhaps such will be true for *Coccotrypes ghesquièrei* Egg., a species we have found in Yangambi only in seeds of Annonaceae, like *Cleistopholis glauca* Pierre ex Engl. et Diels, in *Polyatlthia suaveolens* Engl. et Diels and *Anonidium Mannii* (Oliv.) Engl. et Diels. Another example of this kind may be *Bothryperus quadrioculatus* Egg. a hylesinid so far reported only from Guttiferae, like *Garcinia punctata* Oliv., *Garcinia polyantha* Oliv., and *Pentadesma Lebrunii* Staner. With regard to phloeophagous Scolytidae of higher grades of oliphagy, it is impossible to draw any conclusions at the present time, and the same is true to all African species of Scolytidae and Platypodidae with xylo-mycetophagous feeding habits.

A well known case of a disjunctive oliphagy is reported from the Palaearctic Region. *Polygraphus grandiclava* Thoms. breeds phloeophagously in branches of *Pinus montana* Mill. in the higher altitudes of the European Alps and in twigs and branches of *Prunus cerasus* L. in the low lands.

POLYPHAGY

A host selection within a botanical class is called polyphagy of the first degree, one within hosts belonging to different classes, one of the second degree.

A host selection of this type seems to be lacking in all phloeophagous Scolytidae and apparently also in other insect families with similar feeding habits. Quite different seems to be the principles of host selection in the spermatophagous Scolytidae, especially in the species of the genus *Poecilips* Schauf., which attack a very great number of seeds belonging to plants of quite different positions in the botanical system. In the xylo-mycetophagous Scolytidae, polyphagy is quite common, especially in the tropics, and this is also true for the greater part of the Platypodidae and for the xylo-mycetophagous Brenthidae and Curculionidae. Apparentiy the same conditions are realized in the greater part of truly xylophagous insects, like the Bostrychidae, Anobiidae, Buprestidae, and many Cerambycidae of the tropics.

PANTOPHAGY

Pantophagy, meaning virtually no fixed host-plant relations, supposes that species make no special claims to the quality of food for their development. Such feeding habits are exceptional in the phloeophagous Scolytidae, but they are probably realized in certain small species of the genus *Hypothenemus* Westw. *H. eruditus* Westw. occurs over the tropic and subtropical countries and lives under bark, in more or less decaying wood, in fruits and seeds of an immense number of plants, and has even been found in book covers.

A more restricted pantophagy, meaning one to freshly felled or recently wind-thrown trunks or broken branches of a very large number of trees, sometimes to nearly all species within a certain forest type, is typical of the very common xylo-mycetophagous *Xyleborus mascarensis* Eichh., *Xyleborus ferrugineus* Fab., *Xyleborus torqatus* Eichh., and *Xyleborus perforani* Woll. The first mentioned not only attacks a boundless number of tree-like dicotyledons but has been observed in trunks of *Coccus nucifera* L. and *Neodipsis Baronii* Jum., two monocotyledons, and in a coniferous plant *Thuja* sp. in Madagascar. The same species has been reported from Guatemala and Honduras, breeding there in various species of pines. The list of host plants of *Xyleborus ferrugineus* Fab. certainly will be of the same type, and for the African region we find similar host selection in *Platypus hintzi* Schauf.

BREEDING GALLERIES

There is little doubt that insects breeding under the bark or in the wood of trees evolved gradually, that this evolution took place over a very long period of time, and that not all species reached the same grade of specialization. It seems also to be a fact that breeding habits have become more fixed and less numerous in the temperate zones than in tropical countries. These facts may be related to the number of host-plants available and their distribution. In northern countries we find large areas covered sometimes by a single tree species, or mixed forests with a very limited number of tree-like plants. In the tropics, on the other hand, we ordinarily find, especially in the evergreen rain forest, a huge number of host plants, but the share of a single species in a given area is rather small.

PHLOEOPHAGOUS INSECTS

Buprestidae, Cerambycidae, and certain Curculionidae usually lay their eggs singly or in small groups in crevices of the bark, and the young larvae make irregular galleries, sometimes of a radial type. In other species the females deposit their eggs in small niches made with their mandibles in the bark.

In the Scolytidae the simplest and probably most primitive type of galleries, the cave type, has been observed in species like *Dendroctonus micans* Kugelm. The parent beetles construct only a small nuptial chamber, sometimes a short and often irregular breeding tube, and the females deposit their eggs in irregular patches about the periphery of the cave. The larvae of each egg patch hatch simultaneously and feed one beside the other in columns between the bark and the sapwood. The same type of breeding habits is typical of some

African species like the Cryphaline *Stephanoderes colae* Schedl, *Hypothenemus pusillus* Egg., and *Hypothenemus eruditus* Westw. (Fig. 2) or to the nearctic *Cryphalus amabilis* Chamb., and *Erineosinus squamosus* Blackm.

The majority of other phloeophagous Scolytidae breed in galleries of a distinct pattern (Fig. 1). The radial entrance hole is made by the female, in other species by the male. Within the bark or between the latter and the sapwood, the tunnel is enlarged to a more or less spacious so-called nuptial chamber, probably more often used for turning than for actual mating. From this nuptial chamber one or more mother galleries are constructed by the female or females, while the male is engaged with the removal of sawdust and excrement. From time to time the females interrupt their boring for oviposition. The eggs are deposited in egg niches, small excavations made at the sides of the mother tunnels, sometimes very regularly and alternatively placed sometimes more irregular or situated in small groups here and there. As a rule in each one of these egg niches a single egg is deposited and isolated from the mother gallery by means of boring dust. The hatching larvae begin at once to feed, making the so-called larval tunnels which at the beginning are situated at right angles to the mother galleries, later on with increasing diameter becoming more radial in their arrangement. While the mother galleries of most phloeophagous Scolytidae are kept clean of excrement and boring dust, the larval tunnels are usually densely packed with faeces and wood particles. After reaching maturity, the larvae construct pupal chambers; usually the larval tunnel is greatly enlarged and the walls are fitted with more coarse material. The young beetles may leave immediately, or they may remain for some time in the same tree, feeding in irregularly constructed tunnels until maturity is reached. Other species leave the tree in which they have developed, seek a new host, and excavate food tunnels for the same purpose there, or they may inflict heavy damage until maturity by burrowing at the base of the buds, eating the bark, or tunneling the twigs and killing them.

Differentiation in the composition and pattern of breeding galleries is found in the size, shape, direction, and the number of mother tunnels in a given family, to a lesser extent in the shape of the larval tunnels. Ordinarily each type of gallery is typical of a given species, but it may vary considerably from species to species even within a single genus.

The simplest form of more specialized gallery occurs when the female enlarges the nuptial chamber to a spacious circular cave, and the eggs are deposited in regularly arranged egg niches on the periphery of the latter. The larval tunnels then radiate very regularly, producing a very distinct pattern. This type of gallery seems to be absent or very rare in the Holarctic Region but has been found in two monogamous African Hylesininae: *Styracopterus murex* Blandf. and *Dacryostactus kolbei* Schauf. (Fig. 3). To distinguish this kind of gallery from the common cave type we may call it disc type.

Other monogamous species of Scolytidae construct a single tunnel either parallel to the fibre of the wood (simple longitudinal type) or in a right angle to the fibre (simple transverse type). Both types of galleries are common in the phloeophagous Scolytidae in the Holarctic as well as in Africa (Fig. 3). They are very common in the subfamily Scolytinae, the Xyloctoninae, and in many genera of the Hylesinae but are very rare in the Ipinae.

More variation in the breeding galleries may be found in the bigamous and polygamous Scolytidae in which two, three, and more mother tunnels originate from a common nuptial chamber. In bigamous species the two mother tunnels again may follow the fibre of the

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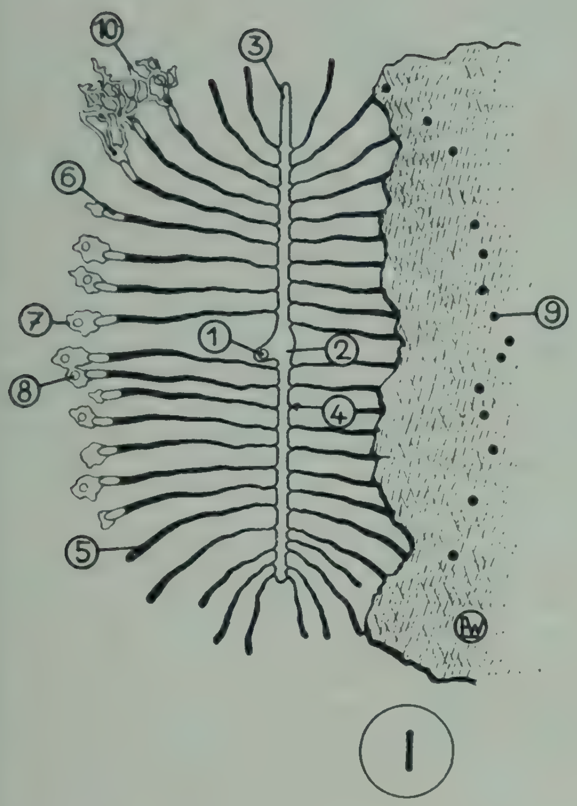
Fig. 1. Schematic sketch of the breeding gallery of a bigamous phloeophagous scolytid. 1, Entrance hole. 2 Nuptial chamber. 3, Mother tunnel. 4, Egg niches. 5, Larval tunnels. 6, Pupal chamber. 7, Feeding of the maturing young beetle. 8, 9, Exit holes of young beetles. 10, Galleries sometimes made by maturing young beetles.

Fig. 2. Schematic sketches of different types of galleries made by primitive phloeophagous Scolytidae. 1, 3, *Hypothenemus pusillus* Egg. and *Stephanoderes ituriensis* Schedl; egg deposition and larval tunnels irregular. 2, *Stephanoderes colae* Schedl; oviposition in patches, larvae feeding in columns. 4, *Hypothenemus parilis* Schedl; oviposition in separated patches, larvae feeding in columns.

Fig. 3. Regular patterns of specialized phloeophagous Scolytidae. 1, Disc type (*Styracopterus murex* Blandf.). 2, Simple longitudinal type (*Hapalogenius congonus* Schedl). 3. Simple transverse type (*Xyloctonus opacus* Schedl). 4, Double circular type (*Mimips angylocalyx* Schedl). 5, Double longitudinal type (*Kissophagus granulatus* Lepesme). 6, Double transverse type (*Bothryperus garciniae* Schedl). 7, Radiate type (*Polygraphus tenuis* Schedl). 8, Radiate longitudinal type (*Polygraphus tenuis* Schedl). 9, Radiate transverse type (*Pityophthorus joveri* Schedl). 10, Radiate bent type (*Chortastus agnatus* Egg.).

wood (branched longitudinal type), run across the fibre (branched transverse type) or curve strongly to form a circle (double circular type) as shown in Fig. 3/3, 5, 6. Fixed types of such branched breeding galleries seem to be typical to certain Hylesinae. Two longitudinal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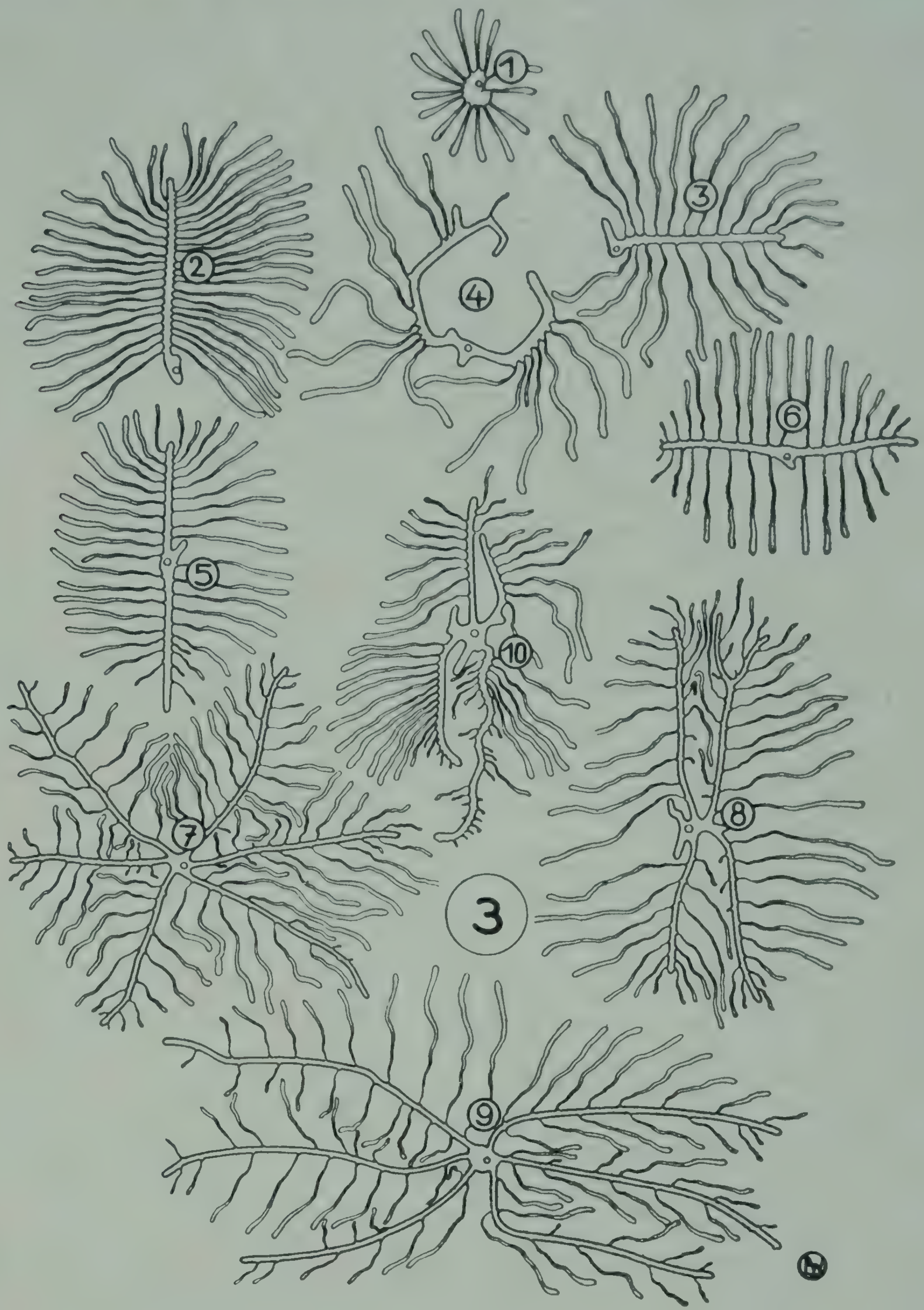
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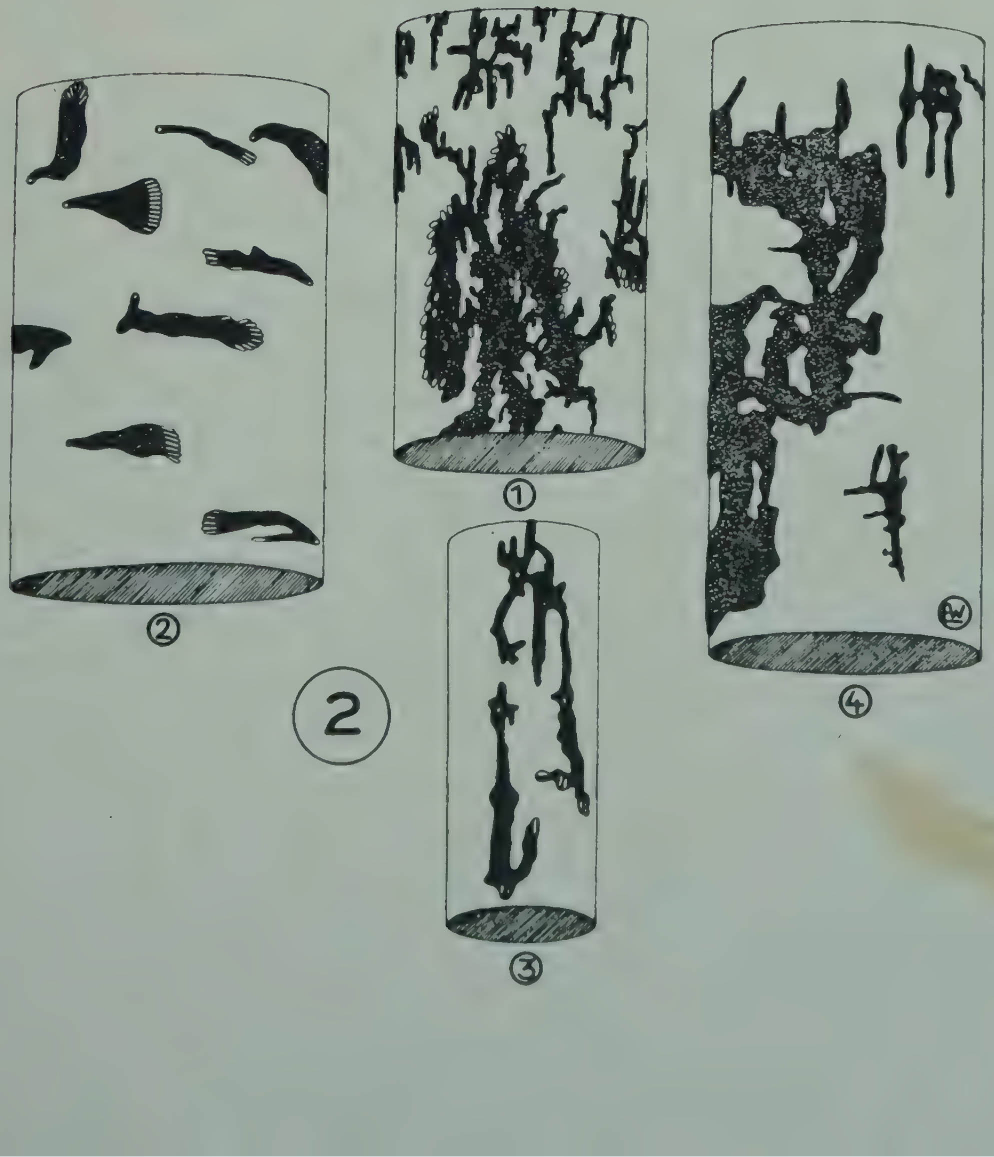
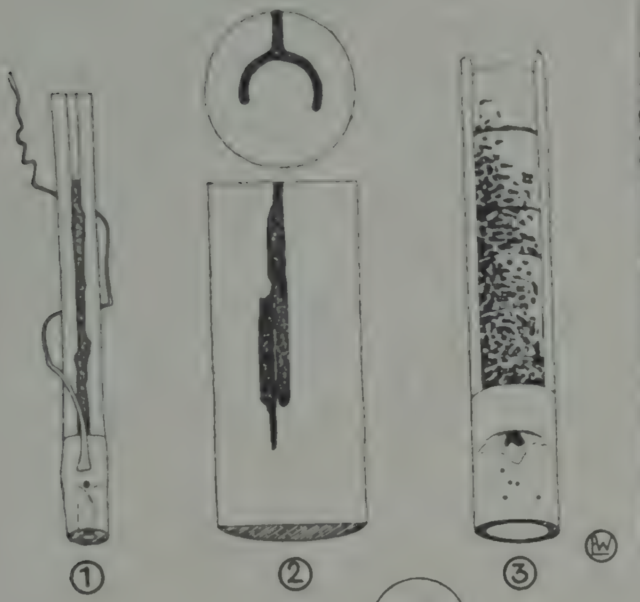
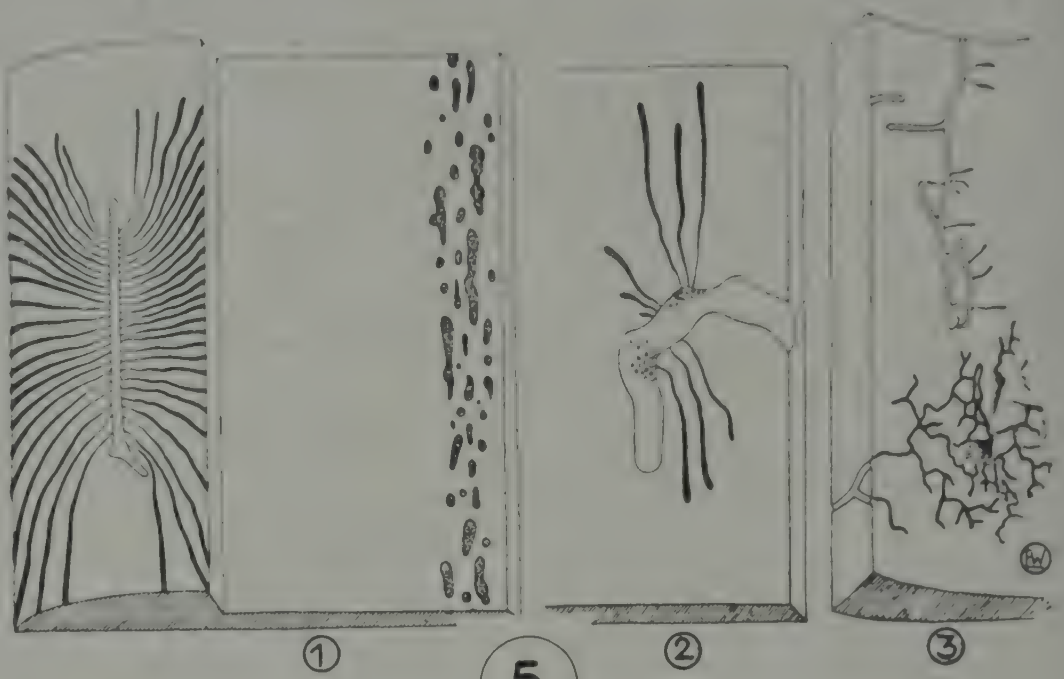


mother tunnels are known in a few species of *Phloeosinus* Chap., *Kissophagus* Chap., from the temperate zones and *Chortastus* Schauf from Africa; two transverse mother tunnels in *Xylechinus pilosus* Ratz. and *Blastophagus minor* Hartig in the Palaearctic Region, in *Pseudohylesinus grandis* Sw. in the Nearctic Region and in *Bothryperus garciniae* Schedl, *Chortastus similis* Egg., to mention a few of them in Africa. Sometimes we find two longitudinal mother tunnels in certain Ipinae, especially in the genus *Ips* Deg., but it seems that in these cases the bigamy is not finally settled, because, besides this type of gallery,





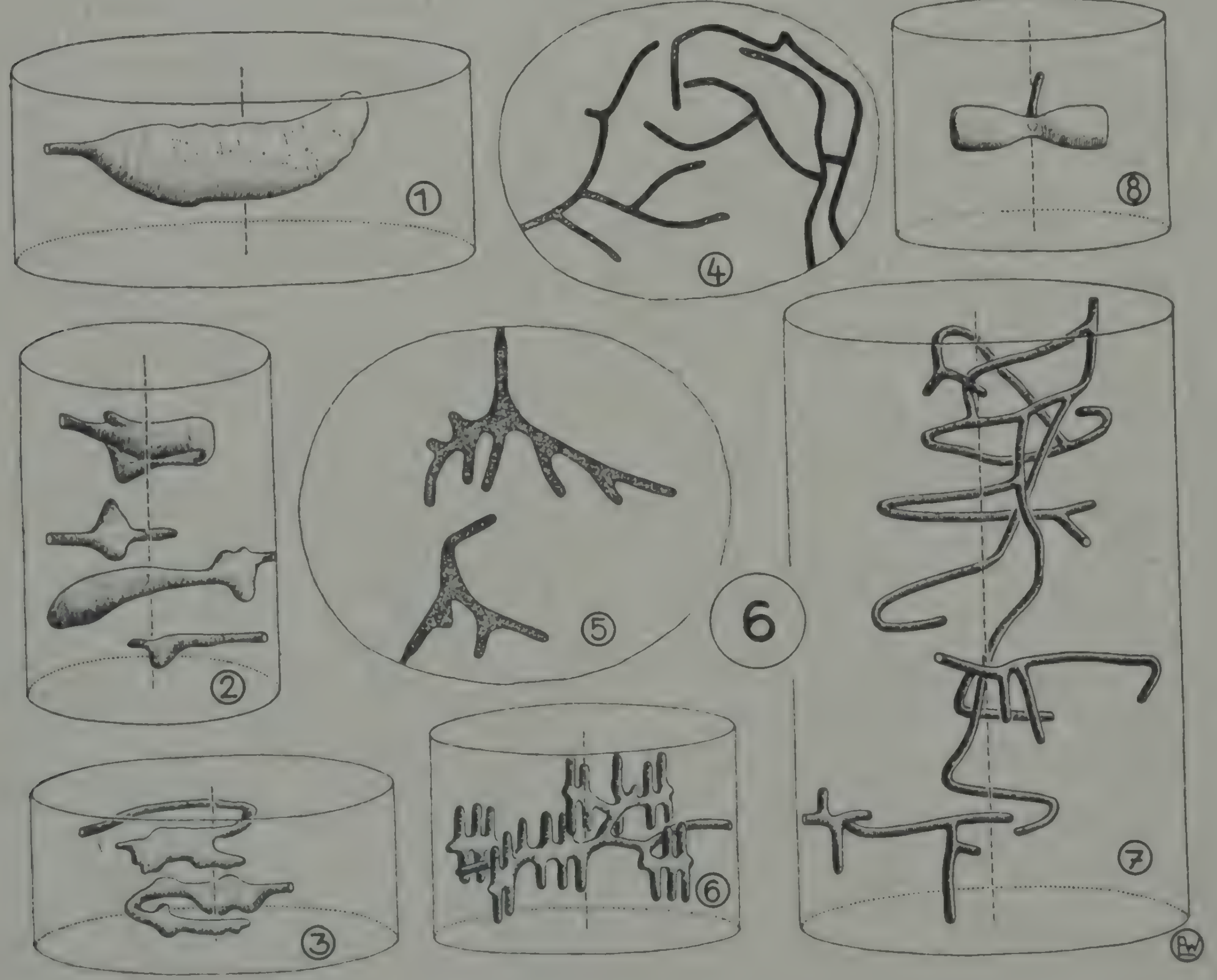


Fig. 4. Breeding patterns of phloeophagous Scolytidae in small twigs and runners of lianes. 1, larval development in the pith (*Lepiceroides aterrimus* Schedl). 2, Three-dimensional larval galleries in the wood of twigs (*Stylotentus ater* Egg.). 3, Larval development on the outside of the pith (*Stephanoderes polyphagus* Egg.).

Fig. 5. Breeding patterns of xylophagous Scolytidae. 1, Intermediate form between xylophagy and phloeophagy; mother gallery, egg niches, and young larvae as in truly phloeophagous species, older larvae and pupae as in truly xylophagous species (*Strombophorus ericius* Schauf.). 2, True xylophagy; mother tunnel hook-like, eggs in irregular patches, larvae entirely xylophagous (*Rhopalopselion grandis* Schedl). 3, Most primitive form of xylophagy; mother galleries, eggs, and larvae without regularity (*Micracidendron montanum* Schedl).

Fig. 6. Different types of breeding galleries of xylo-mycetophagous Scolytidae. 1, Simple pocket type (*Xyleborus comparabilis* Schedl). 2, 3, Irregular pocket types (*Xyleborus agnaticeps* Schedl and *X. cruciformis* Schedl). 4, Ramified tunnel types (*Xyleborus semigranosus* Blandf.). 5, Ramified type with irregular enlargments (*Scolytoplatypus kivuensis* Schedl). 6, Ladder type (*Scolytoplatypus kivuensis* Schedl). 7, Three-dimensional tube type (*Xyleborus alluaudi* Schauf.). 8, Double pocket type (*Xyleborus integer* Schedl).

there usually occur a certain number of breeding patterns with three and even more females, each making its own tunnel. The greater part of the Ipinae, especially the Ipini, Pityophthorini, and the Polygraphini of the subfamily Hylesinae breed polygamously, sometimes with up to six females in one family, producing a corresponding number of mother tunnels arranged either strictly radially; radiate polygamous type (Fig. 3/7), more or less following the fibre of the wood; longitudinal polygamous type (Fig. 3/8); or arranged transverse to the fibre, transverse polygamous type (Fig. 3/9). Still more complicated become the breeding patterns of polygamous species if the mother galleries are not straight but are slightly to strongly curved or bent in one or the other way (Fig. 3/10).

Rather diversified are the breeding habits within the Cryphalini and Crypturgini of the subfamily Ipinae. As many species of them, especially of the Cryphalini develop in very small twigs (Fig. 4), in stems of herbaceous plants, and in fruits and seeds of varying plants, it is often quite difficult to find typical breeding patterns or to decide under which of the various environmental conditions breeding galleries of a fixed type are constructed. As one of the exceptions of this general rule, and because it seems to represent a rather primitive form of a polygamous species, the breeding pattern of *Cryphalomorphus pleiocarpae* Schedl may be discussed. This species appears to construct an irregularly radiating polygamous type in which the entrance hole and the nuptial chamber are used by several females, each of them making its own tunnel as in many species of *Pityophthorus* Eichh. or *Polygraphus* Er. When observed during the oviposition and during the preparation of their tunnels, we note that the males do not follow the females into the tunnels, and the sawdust and the excrement are not removed. The eggs are deposited from time to time either singly or in small groups in the mother tunnel in the sawdust or in egg niches in the walls, which are not so regularly situated as in the polygamous species of the Ipini. Copulation is performed several times during the egg laying period through the exit holes constructed by the females along the mother tunnel. All these irregularities give reason to conclude that the entire breeding habits of *Cryphalomorphus pleiocarpae* Schedl are still in evolution and not finally fixed. Similar habits, but in a somewhat more progressed stage, have been found in certain African species of the genus *Polygraphus* Er.

XYLOPHAGOUS INSECTS

In general, many of the xylophagous Cerambycidae, Buprestidae, Bostrychidae, Anobiidae, etc., have not specialized to develop distinct gallery types, and in many cases it is rather difficult to draw conclusions from a given piece of wood concerning the insect species. The eggs are deposited either in crevices of the bark, in primitive egg niches made in the bark or in the wood itself, and the larval galleries are rather confused. In spite of these well known facts some very interesting breeding habits have been found in Central Africa, which may throw some light on the phylogenetic development of the different insect families concerned.

Some xylophagous Bostrychidae, like *Xyloperthodes nitidipennis* Murray and *Xylopertha piceae* Oliv., usually show no distinct gallery type but may change their breeding habits when developing under certain conditions in the untouched African rain forest. In freshly felled trees they may construct a simple longitudinal breeding tunnel between bark and sapwood like many monogamous Hylesinae and may lay their eggs in regular egg niches as in most of the phloeophagous Scolytidae. The hatching larvae feed in regular larval tunnels during the first part of their development and become truly xylophagous in the second half of their lives when they leave the zone between the bark and sapwood in order to enter the wood itself. A very similar change from phloeophagy to xylophagy during larval life exists among certain African Hylesinae like *Strombophorus ericius* Schauf. (Fig. 5/1), with the only difference that the parent beetles make absolutely normal tunnels and the egg niches are more regularly arranged.

A cossonid (not determined), on the other hand, has been observed in branches of *Xylopia Wilwerthii* De Wild. developing during the entire larval stage in a truly xylophagous manner, with a breeding gallery corresponding in many details to the simple longitudinal type of phloeophagous Hylesinae, except that it was situated in the wood itself. The mother tunnel followed the fibre from 6 to 12 mm. under the surface of the wood; the larval tunnels remained at the same level; and the egg niches were arranged rather regularly. Similar arrangements of the entire system may be found in *Strombophorus* *milletiae* Schedl when breeding in the liane *Millettia Duchesnei* De Wild., showing once more the close relation in breeding habits between the Curculionidae and certain Scolytidae.

A third degree of specialization towards a true xylophagy occurs when the female enters the wood in order to construct a rather irregular hook-like tunnel, depositing the eggs not in regularly arranged egg niches but singly or in small groups here and there (Fig. 5/2). This type is rather common in tropical and Holarctic Bostrychidae, Anobiidae, and Cossonidae. Again we found some parallels in African Scolytidae, as in *Metahylesinus horridus* Egg. and *Rhopalopselion grandis* Schedl. In *Micracidendron montanum* Schedl, the type of the breeding gallery is so similar to those of certain Bostrychidae, Anobiidae, or Cossonidae that it would be impossible to determine the insect by examining the wood samples only. All these facts clearly show that the relationship of these coleopterous families, usually based on morphological characters, holds true if the breeding habits are considered. It certainly would be very interesting to enlarge these investigations by a thorough study of the digestive channel of these groups, especially the proventriculus.

Xylo-Mycetophagous Insects

In the highest degree of specialization of wood-boring insects, in xylo-mycetophagy, breeding galleries can be reduced to a minimum, as not the wood itself serves as a source of nourishment, but the fungi growing on the walls of the tunnels. This purely theoretical consideration actually is realized in all groups of xylo-mycetophagous feeding habits.

In the Lymexylonidae, in the well known Palaearctic of *Hylocoetes dermestoides* L., the females lay their eggs singly in crevices of the bark, and each hatching larva constructs its own tunnel feeding continuously on the mycelium of the fungi, which are cultivated on the walls. Probably this type of breeding tunnel of the progeny is the most primitive so far observed. An African representative of the same type seems to be the well known "scorpion volant", *Atractocerus brevicornis* L.

The tunnels in which the development of xylo-mycetophagous scolytid larvae takes place are exclusively made by the parent beetles. The possibilities of variation within this group are rather limited also by the fact that in many species, especially within the huge xylo-mycetophagous Xyleborini, the males do not take part in the construction of the the breeding tunnels, but die after copulation has taken place in the old galleries of the parents. A further simplification is reached when, as in certain Brenthidae and Curculionidae, the females do not make the entrance holes themselves but use those of xylo-mycetophagous Scolytidae and Platypodidae, restricting their breeding activities to the preparation of egg niches and the deposition of eggs.

Returning to the xylo-mycetophagous Scolytidae, we find the simplest and most primitive breeding galleries in some species of the genus *Xyleborus* Eichh. In these examples the females simply make a radial entrance hole, enlarging it within the outer layer of the wood to a pocket-like cave in which from time to time the eggs are deposited in small groups freely on the periphery of the cavity. (Fig. 6/7). In this xylo-mycetophagous cave type, one can find after a certain time all stages of development from freshly laid eggs to young beetles ready for emergence, while the mother lives among her progeny or closes the entrance hole against parasites and predators with her body, very often dying in this position. Such pocket-breeding species are typical for at least two groups of the genus *Xyleborus* Eichh., the Xylebori angustati and Xylebori ephipiger, the first widely distributed over tropical countries including Africa, the latter endemic to this continent. *Xyleborus integer* Schedl, another African species, forms a double pocket with the entrance hole in the center, probably a first step to a higher type of specialization (Fig. 6/8).

In all other species of *Xyleborus* known, the breeding pattern consists of more or less ramified circular breeding tunnels exclusively made by the females. The ramification again may be realized in a single level across the fibre of the wood or in three dimensions as shown in Fig. 6/7. Within one species the tendency may exist to breed in simple ramified tunnels in large trunks while, when development takes place in smaller branches or twigs, the ramification becomes three-dimensional, some of the tunnels extending along the fibre of the wood. In still smaller branches and twigs the entire breeding pattern may be drawn out more longitudinally, without any regular arrangement. In all these cases the eggs are deposited by the females freely in the breeding tunnels, and larval development takes place under the same circumstances. Oviposition again goes on from time to time, while the females continue the construction of new branches. The resulting progeny varies in its stage of development, pupation occurring among eggs and larvae of different ages.

A higher grade of specialization is reached when the eggs are deposited in regularly placed niches on the lower and upper walls of the ramified breeding tunnels. This type only has been observed in species in which both parents take part in the construction of the breeding tunnels. This is the case in *Trypodendron* Steph., *Xyloterinus* Sw., and *Dendrotrypum* Schedl. The hatching larvae enlarge the egg niches into short cup-like tunnels as they increase in size. Pupation takes place when these tunnels reach the length of the full grown larvae. The African species of *Scolytoplatypus* Schauf. breed in similar galleries (Fig. 6/6) but may simplify their pattern under certain circumstances (Fig. 6/5) and between these two extremes one can find all intermediate forms.

In the Platypodidae we find a similar plasticity in breeding galleries. The eggs are laid freely in the breeding tunnels, and larval development goes on under the same conditions. The breeding tunnels as a rule are circular in cross section; more rarely pocket-like enlargements are present, as this has been observed in *Doliopygus conradti* Strohm. in the Belgian Congo (Fig. 7/2). The entire system of breeding galleries in the Platypodidae is much more drawn out in all three dimensions. Probably this extension in space can be explained by the fact that, in this family, both sexes are actively engaged in the formation of the breeding tunnels, the females working on the end of the breeding tubes, the males removing the sawdust, keeping the tunnels clear for communication, and taking care for the ventilation.

The majority of the Platypodidae breed in three-dimensional ramified galleries of a very similar type without any specific characteristics. Once in a while larval development and pupation take place in short tunnels along the fibre exactly as in *Trypodendendron* Steph., but it is not certain that the type of oviposition also corresponds to the habits realized in that genus. This divergence from the rule seems to be not connected with the host plants, the dimensions of the breeding material, or to certain species within Platypodidae. Probably it represents a first step to further specialization. Another variety has been observed in the genus *Platyscapulus* Schedl in which similar but distinctly longer longitudinal tunnels are constructed by the females. In these tunnels two, three, or even more larvae develop, and one pupa is separated from the next by sawdust plugs (Fig. 7).

While in the phloeophagous species each family lives entirely separated from the other, communication tunnels between the galleries of various families are rather common in xylo-mycetophagous species. This has been observed in two dimensional ramified breeding galleries in very large trunks as well as in branches in which the breeding galleries of a single family extend into three dimensions. In this way communication is possible between the parent beetles of many families as well as for their progeny, sometimes over very long parts of branches or smaller trunks (Fig. 8).

At the top of the development of xylo-mycetophagous insects we are certainly justified in placing certain Brenthidae and Curculionidae. In both families this high stage is found in certain tribes or genera only, like the Calodromini, the Taphroderini and Pseudocephalini of the Brenthidae, and the genera *Scolytoproctus* Marsh. and *Curaniger* in the Curculionidae. As already mentioned none of these species actively take part in the construction of breeding galleries but, as in the case of the cuckoo, use the nest, meaning the entrance tunnels of Platypodidae and Scolytidae, to deposit their eggs, usually in some kind of egg niches on the periphery in a depth of 1 to 2 cm. within the wood. It also seems to be evident that at least in some cases they expel their host and sometimes become so predators on them. The young larvae make their own tunnels, like those of the larvae of Trypodendron Steph., short, not longer than the length of the future young beetle (*Scolytoproctus, Curaniger*), or as in the Lymexylonidae, very long, the larvae moving forth and back in feeding on the fungi cultivated on the walls. Pupation in both cases takes place in these tunnels, with the head directed to the entrance tunnel of the host, and the young beetles leave by removing the plug which has separated their larval tunnels from the entrance tube of the host.

SUMMARY AND CONCLUSIONS

It is obvious that wood inhabiting insects at the very start of their development were saprophagous or necrophytophagous, entering their hosts when decay of the wood already had commenced. They certainly were polyphagous at first and most probably

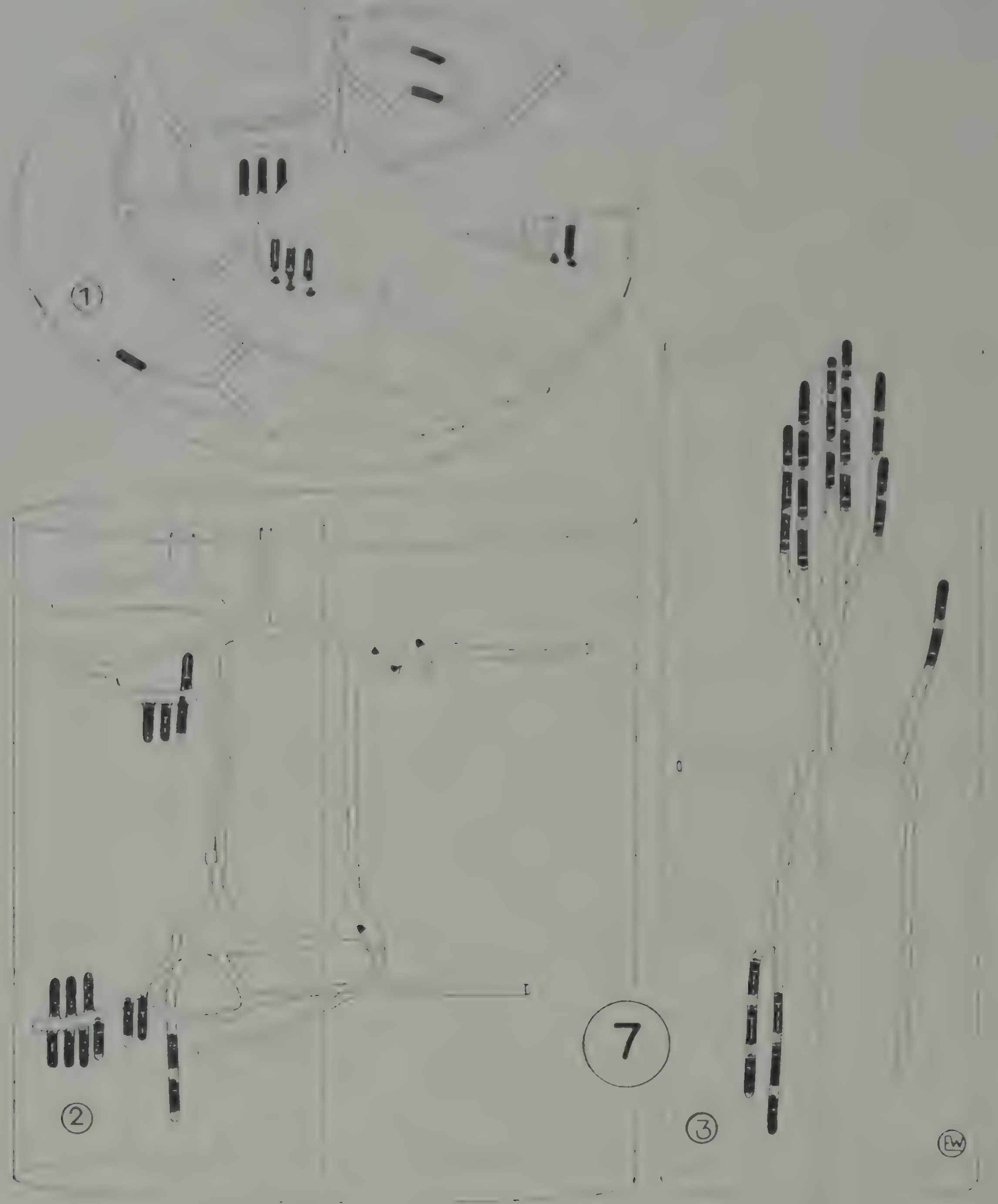


Fig. 7. Breeding galleries of Platypodidae. 1, Two-dimensional tube type with some ladder-shaped larval tunnels (*Doliopygus bitalei* Schedl). 2, Three-dimensional type with irregular enlargments and ladder-shaped larval tunnels (*Doliopygus conradti* Strohm.). 3, Ramified galleries along the fibre with pupae in rows (*Platyscapulus granulosus fratellus* Schedl).

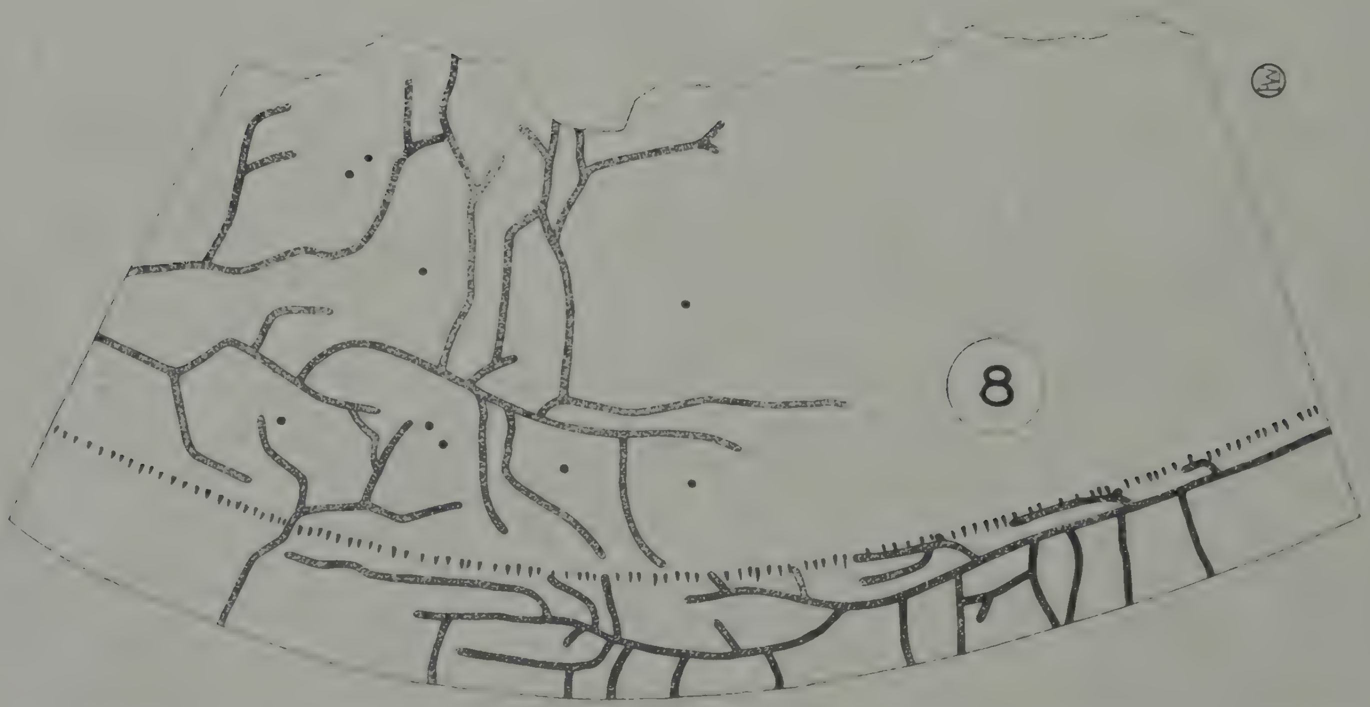


Fig. 8. Several breeding galleries of *Xyleborus badius* situated on one level across a large trunk and partly connected to one another, showing at right a preference for the outer layers of the wood.

monogamous. Their breeding habits were very simple, and they did not follow a specific pattern in making their breeding tunnels, if they made them at all, and the eggs were laid without any regularity. The larvae fed in the wood, making their tunnels irregularly here and there as we find them today in necrophytophagous Lucanidae, Prioninae, Anobiidae, Bostrychidae, etc. In the Scolytidae of today such primitive breeding habits are found in the phylogenetically old Hylesinae, very exceptionally and probably secondary in the more modern Ipinae. All such species and higher systematic units with this primitive breeding habits feed xylophagously, as far as we know, breaking up wood substance by the aid of extracellular entosymbiontes living freely in the digesting channel or in special enlargements of it.

The second stage of nutrition was reached when the larvae began to develop in the cambium of the bark, a layer extremely rich in nutritive substances of highest value. Hand in hand with this specialization, a gradually growing of differentiation in the breeding habits of the parent beetles occurred. In the first step, the eggs may have been laid in the cambial region of the entrance hole, later in enlargements now called nuptial chambers, and finally in special tunnels originating from the nuptial chamber. Within the same period of time another step in oviposition may have taken place, as the early irregular deposition of the egg here and there on the walls was replaced by regularly arranged egg niches, giving every hatching larva the same ecological chance for development. The final development of these phloeophagous insects led to bigamy and polyphagy, producing at the same time several new patterns of breeding galleries. All these different stages in the phylogenetic rise of breeding habits still can be observed within the Scolytidae, more completely in the African Hylesinae than in the Palaearctic or Neartic Regions. How far intracellular entosymbiosis is typical of the different stages of phloeophagy has not been investigated.

The third and final specialization of wood inhabiting insects is realized in xylomycetophagy. This stage of development has been reached by several families of Coleoptera, in the most primitive form in the Lymexylonidae, in the highest level in the Platypodidae and certain genera and groups of Scolytidae and in a space-parasitic form in certain Brenthidae and Curculionidae.

Preliminary Evidence for Gene Flow among North American Populations of *Tropisternus mexicanus* (Castelnau) (Coleoptera: Hydrophilidae)

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ABSTRACT

Three populations of Tropisternus mexicanus *(Castelnau) are recognizable in northern Mexico and the United States. These have been designated as allopatric subspecies:* mexicanus mexicanus *in northern Mexico, extending into Texas, Oklahoma, Kansas, and Missouri;* m. striolatus *(LeConte) in the eastern United States; and* m. viridis *Young and Spangler in Florida and southeastern Georgia. A study of the chemical nature of the pigment of the elytra, pronotum, and head indicates that the various patterns are probably controlled by series of polygenes and are not the direct effect of environment. Along the borders of the ranges of the three subspecies, mixed populations occur, and different distances of penetration can be measured for what seem to be gene-based elements of the color patterns. Rearing experiments are now in progress to determine the genetic basis. It is hoped that the completed study will furnish material for the quantitative analysis of the action of selection and the interaction of genetic and environmental factors.*

The Phyletic Significance of the Female Internal Organs of Reproduction in the Elateridae[1]

By Edward C. Becker[2]
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ABSTRACT

A preliminary survey of the female internal organs of reproduction in the Elateridae indicates the presence of many useful characters that are helpful in studying the phylogeny. Structures such as the sclerotized plates and the number and position of glands on the bursa copulatrix apparently provide a sound basis for regrouping the species, at least in the genera Agriotes, Limonius, *and* Hypolithus. *In many cases these structures do not show specific differences; however they do permit grouping of certain species. Similar structures are found in other coleopterous families.*

The study of the female internal organs of reproduction is certainly by no means new. These structures were described extensively as early as 1847 (Stein), but very few workers have used them in a phyletic study. Usually authors have described and illustrated these organs for isolated species.

The work that I have done is mostly preliminary, but I feel that the internal organs may assist in the solution of some of the phyletic problems in the elaterids. Whether or not you agree with my conclusions as to the usefulness of these organs, the fact remains that very few workers have even taken the time to examine these structures.

Contrary to what many previous workers have stated, I have found that pinned specimens usually make as good preparations as fresh ones. Briefly my technique is to remove the abdomen and clear it in ten per cent cold KOH for an hour or so. When placed in water the abdomen usually swells so that the tergites and sternites can easily be separated with a small knife. The tergites and attached internal organs may be replaced in the KOH for another hour if necessary. When placed in water the reproductive organs inflate so that it is easy to remove the tracheae, digestive tract, matrix, etc. If handled carefully the various glands and spermatheca will remain intact. The KOH destroys the ovaries; however the base of the median oviduct remains. The dissection is stored in a microvial containing glycerin.

The glands vary in number, size, and shape and are difficult to homologize in some cases. There are two structures that can be used to orient the reproductive system: the base of the median oviduct, which is between the colleterial glands, and the peculiar attachment of the spermatheca to the spermathecal duct (Fig. 7). In most of the elaterids I have examined this connection is present; in other cases I have been unable to find it probably because it is delicate and easily broken.

The colleterial glands may be elongate (Fig. 7) or simply enlargements of the vagina (Fig. 8). The bursa copulatrix is the most heavily sclerotized area and frequently has various spines and plates (signa of the lepidopterists). There is usually one accessory gland arising from the bursa copulatrix. The shape and position of the accessory gland varies between groups of species. Also there is usually a gland or group of glands attached near the spermatheca that I call the diverticulum of the spermathecal duct. In the elaterids the spermatheca is membranous and very delicate and has several branches. In contrast, some coleopterous families have the spermatheca heavily sclerotized.

The results of a recent study of *Agriotes* (Becker, 1956) are briefly summarized here. By using the female internal organs of reproduction as the main basis for grouping the species I have arrived at certain phyletic conclusions that are not so apparent by a study of other characters. A study of the male genitalia and external features of the adults and larvae substantiated the conclusions stated below. The subtribe Agriotina contains three genera, *Dalopius*, *Agriotella*, and *Agriotes*. The genus *Agriotes* can be divided into four groups, *criddlei*, *limosus*, *sputator*, and *sparsus*. The long saclike colleterial glands are characteristic of this subtribe, although they also occur sporadically in other tribes. Most of the

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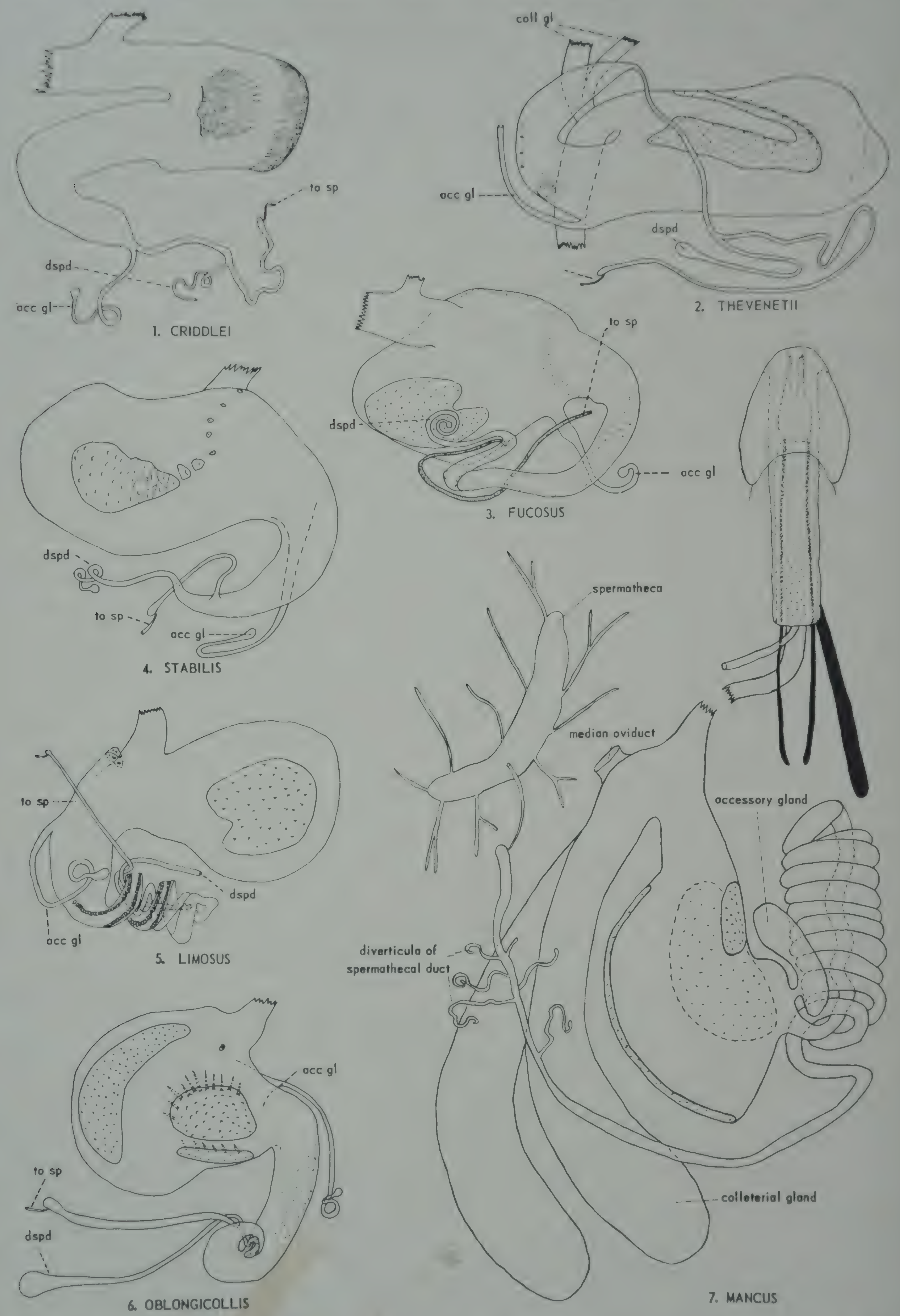
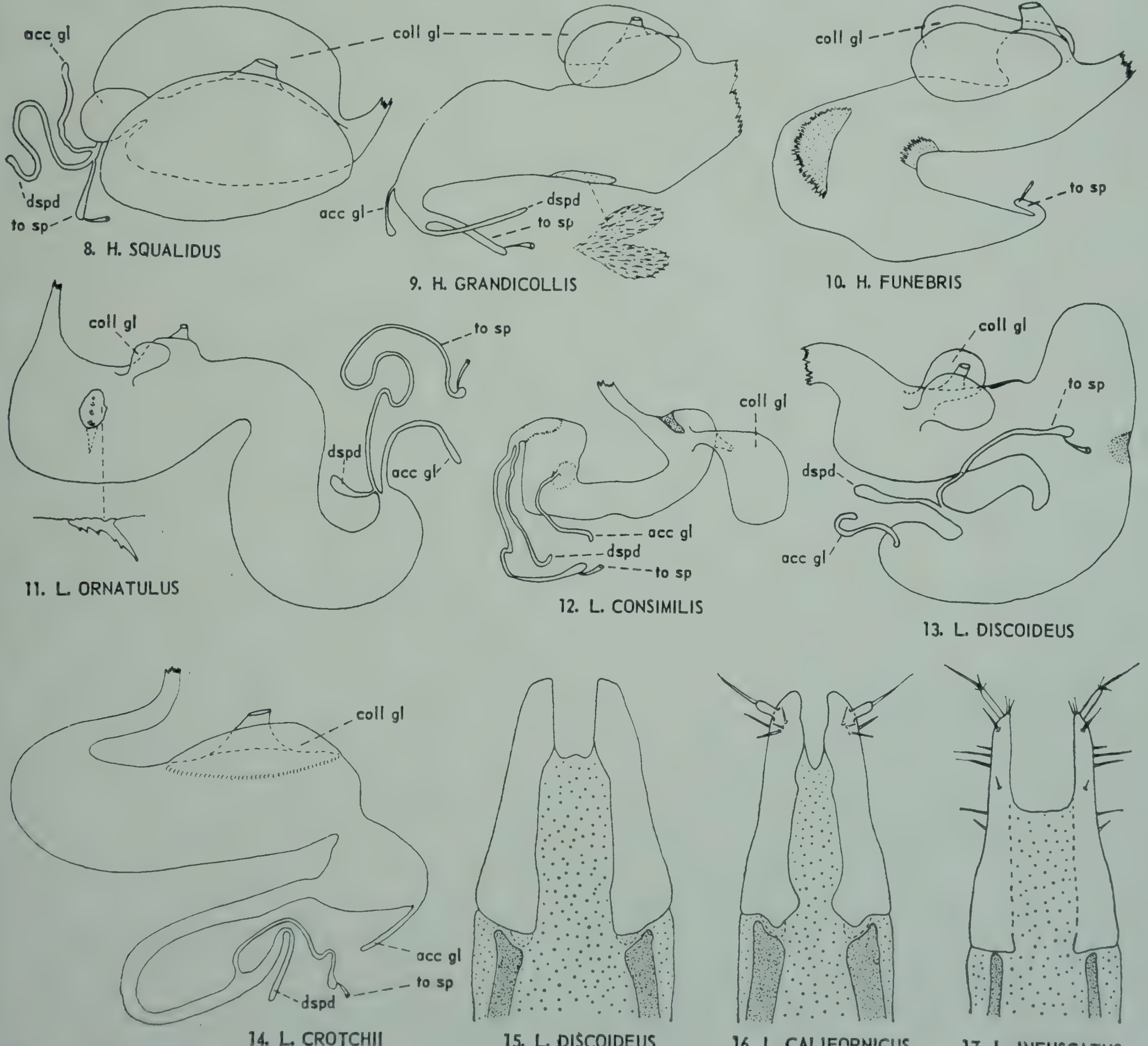

to sp
dspd
acc gl
1. CRIDDLEI
coll gl
acc gl
dspd
2. THEVENETII
to sp
dspd
acc gl
3. FUCOSUS
dspd
to sp
acc gl
4. STABILIS
spermatheca
median oviduct
to sp
dspd
acc gl
5. LIMOSUS
accessory gland
diverticula of spermathecal duct
acc gl
to sp
dspd
6. OBLONGICOLLIS
colleterial gland
7. MANCUS

Figs. 1–7. *Agriotes* spp., female internal organs of reproduction. Acc gl, accessory gland; coll gl, colleterial gland; dspd, diverticulum of spermathecal duct; to sp, to spermatheca.

species of *Dalopius*, all of the species of *Agriotella*, and the *criddlei* group of *Agriotes* [*criddlei* Van Dyke and *bivittatus* Van Dyke] have essentially the same type of female internal organs of reproduction (Fig. 1), that is, the accessory gland does not join directly to the bursa copulatrix and plates are unlike those of the other groups. These species are related, although I believe they form three genera based on other characters.

The species of the *limosus* group (Figs. 2–6) are characterized by having the colleterial glands about as long as the bursa copulatrix, a long narrow accessory gland, only one diverticulum on the spermathecal duct, and plates of various sizes and shapes, but never like those of the other groups. Four species (Fig. 4) have a pair of irregularly shaped plates [*hoodi* Becker, *quebecensis* Brown, *stabilis* (LeConte), and *ferrugineipennis* (LeConte)]. Three species (Fig. 3) have a pair of slightly notched regularly shaped plates [*brunneus* Schaeffer, *fucosus* (LeConte), and *collaris* (LeConte)]. Two species (Fig. 5) have a pair of slightly notched regularly shaped plates and also a small single one [*tardus* Brown and *limosus* (LeConte)]. Three species (Fig. 2) have a pair of deeply notched regularly shaped plates, as well as a small one [*avulsus* (LeConte), *thevenetii* Horn, and *torquatus* LeConte]. Finally, three species (Fig. 6) have two pairs of plates, one pair with long spines and the other with short ones [*oblongicollis* (Melsheimer), *arcanus* Brown, and *espinosus* Becker]. The European *aterrimus* (Linnaeus) and all of the eastern Palearctic species that I have examined, except *elegantulus* Lewis, also belong to the *limosus* group.

The internal organs of reproduction of the *sputator* group are of the same type (Fig. 7) and are characterized by having the colleterial glands about twice as long as the bursa copulatrix, the accessory gland short and thick, the plates on the bursa copulatrix of the same general shape, the base of the spermathecal duct coiled, and there are several diverticula on the spermathecal duct. Four native Nearctic species [*insanus* Candèze, *pubescens* Melsheimer, *belfragei* Becker, and *mancus* (Say)] belong to the *sputator* group,



8. H. SQUALIDUS

9. H. GRANDICOLLIS

10. H. FUNEBRIS

11. L. ORNATULUS

12. L. CONSIMILIS

13. L. DISCOIDEUS

14. L. CROTCHII

15. L. DISCOIDEUS

16. L. CALIFORNICUS

17. L. INFUSCATUS

Figs. 8–14. Female internal organs of reproduction. Figs. 8–10, *Hypolithus* spp. Figs. 11–14, *Limonius* spp. Acc gl, accessory gland; coll gl, colleterial gland; dspd, diverticulum of spermathecal duct; to sp, to spermatheca. Figs. 15–17. *Limonius* spp., female external genitalia.

as do all of the Central American species, all of the European species except *aterrimus*, and *elegantulus* Lewis from Japan. Two European species [*acuminatus* (Stephens) and *pallidulus* (Illiger)] are of particular interest since they have certain external characters of the *sparsus* group, but they have the same internal organs of reproduction as attributed to the *sputator* group; thus they form a connecting link between these groups.

The species of the *sparsus* group are grouped together because of the lack of plates on the bursa copulatrix. These species are: *sagittus* Becker, *sparsus* LeConte, *isabellinus* (Melsheimer), *longithorax* Becker, *cylindricus* Van Dyke, *oregonensis* Becker, *imperfectus* LeConte, *rotundicollis* Becker, and *vandykei* Becker.

The genus *Limonius* can be divided into four groups and several isolated species. I have not made as complete a study of this genus, nor of *Hypolithus*, as I have with *Agriotes*, however a preliminary study indicated that these internal structures may form the basis for grouping the species. These genera are in need of a revisionary study and therefore the names I am using are more for convenience than for nomenclatural purposes.

One group of *Limonius* containing four species (Fig. 11) has a pair of spiny plates and the accessory gland is near the base of the spermatheca as illustrated [*definitus* Ziegler, *humeralis* Candèze, *nimbatus* (Say) and *ornatulus* LeConte]. Two species have one plate anterior to the colleterial glands and two weakly sclorotized rings around the base of the accessory gland and the spermathecal duct (Fig. 12) [*consimilis* Walker and the European *aeneoniger* (De Geer)].

Another group containing 11 species (Fig. 14) is characterized by the lack of plates and the rather small bursa copulatrix. Included in this group are *bicolor* Van Dyke, *confusus* LeConte, *crotchii* Horn, *fulvipilis* Candèze, *griseus* (Beauvois), *pictus* Van Dyke, *plebejus* (Say), *rufihumeralis* Lane, *stigma* (Herbst), *ulkei* Horn, and *venablesi* Wickham.

Another large and difficult group has similar internal structures as illustrated (Fig. 13), but very different female external genitalia. Five species have a heavily sclerotized genitalia (Fig. 15) that is devoid of setae [*agonus* (Say), *anceps* LeConte, *discoideus* LeConte, *subauratus* LeConte, and *subcostatus* Motschulsky]. Three species (Fig. 16) have a small subapical lobe and a few setae near the apex [*californicus* (Mannerheim), *canus* LeConte, and *dubitans* LeConte]. Four other species (Fig. 17) have the usual elaterid type of genitalia, that is, weakly sclerotized with a long apical lobe and several setae on the apical two-thirds [*infuscatus* Motschulsky, *pilosulus* (Candèze) *vernalis* Fall, and an unidentified species near *subauratus*].

I have examined six other species but apparently none of them belong to any of the above groups [*aeger* LeConte, *aurifer* LeConte, *basillaris* (Say), *nitidulus* Horn, *quercinus* (Say), and *rudis* Brown]. The other species of *Limonius* have not been examined because females were not available.

The species of *Hypolithus* apparently fall naturally into three groups. At least five species (Fig. 8) have a small bursa copulatrix without plates and large colleterial glands [*abbreviatus* (Say), the *bicolor-nocturnus* complex, *impressicollis* (Mannerheim), *littoralis* Eschscholtz, and *squalidus* (LeConte)]. Two species (Fig. 9) have a single plate [*glacialis* (Van Dyke) and *grandicollis* (LeConte)]. The last group, containing four species, has a pair of plates as well as a single one (Fig. 10) and lacks the accessory gland and the diverticulum on the spermathecal duct [*funebris* (Candèze), *hyperboreus* (Gyllenhal), *lecontei* (Leng), and *sanborni* (Horn)].

These proposed groupings for *Limonius* and *Hypolithus* are somewhat different from those found in the current catalogues. The difference between my grouping of the species of *Hypolithus* and that of Horn (1891) can readily be illustrated.

grandicollis
hyperboreus
sanborni
funebris
Horn's grouping *lecontei* Present grouping
squalidus
abbreviatus
impressicollis
bicolor-nocturnus
littoralis

A preliminary survey of the male genitalia of the species of *Hypolithus* indicates the same grouping as does the female reproductive organs. I believe that a re-study of the external features of the adults and those of the larvae may also substantiate these proposed groupings.

I have examined representatives of most of the Nearctic genera of elaterids and feel that the use of the female internal organs of reproduction may assist in studying the phylogeny of this family. In his summary, Binaghi (1955) stated, "The author proposes a new classification of *Cardiophorus* based especially on the characters of the female genitalia apparatus (bursa copulatrix) which contains morphological elements that allow one to demonstrate the phylogenetic affinities of the various groups of this complex genus". This is precisely the same conclusion at which I arrived for the species of *Agriotes* and very likely reflects what may be found in other genera.

Structures similar to those described above occur in other families of Coleoptera. Stein (1847) was probably the first to illustrate the female internal organs of reproduction to any extent. He treated over 100 species representing many families. Williams (1945) did the same, but with a much smaller number of species. Schweiger (1952), for example, suggested that these structures were useful in the carabid genus *Trechus*. The differences found in other families suggests that these internal organs may be useful in studying the phylogeny of various groups.

REFERENCES

Becker, Edward C. 1956. Revision of the Nearctic species of *Agriotes* (Coleoptera: Elateridae). *Canadian Ent.* 86, Supplement 1: 101 pp., 74 figs.

Binaghi, G. 1955. Ricerche zoologiche sul massiccio del pollino (Lucania-Calabria). XII. Coleoptera. 2. Elateridae, Melasidae, Throscidae e Dascillidae. *Annuario dell'Istituto e Museo di Zoologia dell'Universita di Napoli* 7: 1–19, 11 figs.

Horn, G. H. 1891. A monograph of the species of *Crytohypnus* of Boreal America. *Trans. American Ent. Soc.* 18: 1–31, 1 pl.

Schweiger, H. 1952. Der weibliche Genitalapparat der Gattung *Trechus* (Col., Carabidae) und seine Bedeutung für die Systematik. *Trans. Ninth Int. Congr. Ent.* 1: 127–129, 2 figs.

Stein, F. 1847. Vergleichende Anatomie und Physiologie der Insecten in Monographien bearbeitet. Erste Monographie. Die weiblichen Geschlechtsorgane der Käfer. *Duncker und Humblot,* Berlin. viii + 139 pp., 9 pls.

Williams, J. L. 1945. The anatomy of the internal genitalia of some Coleoptera. *Proc. Ent. Soc. Washington* 47: 73–91, 9 pls.

Blind Beetles in the Fauna of the Pacific Northwest

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ABSTRACT

The Pacific Northwest contains only a few small limestone caverns and, so far, no endemic beetles, blind or otherwise, have been found in them. The blind species belong to three groups: Anilloferonia *with four species in Carabidae;* Catopocerus *with eight species in Leiodidae; and the Leptinidae with three species in as many genera.* Anilloferonia *and* Catopocerus *live under dense cover on the ground; the Leptinidae are ectoparasites of mammals.*

Since their discovery in European caves in the second quarter of the last century, blind beetles have greatly excited the interests of coleopterists in all parts of the world. Along with other cavernicolous animals, they furnished a prime example of adaptation to a peculiar environment and also gave the Lamarckians a classic case of the so-called evolutionary effects of disuse. In view, then, of these several circumstances, it seemed as though a brief discussion of the blind beetles in the fauna of the Pacific Northwest might be of some general interest. By Pacific Northwest I mean British Columbia, Washington, Idaho, and Oregon — the area between Alaska and California.

Up to the present time no cave beetles have been discovered in the Pacific Northwest. Limestone caves are of limited occurrence in that part of the world; and, such as there are (Oregon Caves, 52 miles southwest of Grant's Pass, Oregon; Gardner Cave, north of Metaline Falls, Washington), have so far produced no blind beetles.

The blind beetles known to me that occur in the fauna of the Pacific Northwest belong to three taxonomic groups: (1) the genus *Anilloferonia* Van Dyke, related to *Pterostichus* in the family Carabidae; (2) the genus *Catopocerus* Motschoulsky, variously placed in the Silphidae, Catopidae, or Leiodidae; and (3) the genera *Leptinillus* Horn, *Leptinus* Muller, and *Platypsyllus* Ritsema, variously placed in the Silphidae or in a separate family, the Leptinidae. *Anilloferonia* and *Catopocerus* live in the humus of the forest floor of the rain forests that are so characteristic of the area west of the Cascade Mountains in the Pacific Northwest and have apparently become blind in response to their burrowing habits. *Leptinillus*, *Leptinus*, and *Platypsyllus* are ectoparasites of mammals, and their loss of functional eyes is apparently part and parcel of the general degeneracy of structure to which parasites are liable.

The diagnostic characters of the four species of *Anilloferonia* are set forth in Part I of *The Beetles of the Pacific Northwest* published in 1953 (Hatch, 1953); and the diagnostic characters of the Northwestern species of *Catopocerus* and Leptinidae will be found in Part II of the same work (Hatch, 1957).

In addition to these three groups of anophthalmous beetles, Wickham in 1890 (Wickham, 1890:88) recorded the blind Californian Tenebrionid, *Alaudes singularis* Horn, from an ant's nest at Huntington in eastern Oregon. I have not had the opportunity to study this species and no further mention of it will be made here except to call attention to the fact that the ant's nest is another highly specialized habitat in which it is quite conceivable that a blind social parasite or symbiote would be able to function.

Before discussing each of these groups of eyeless beetles in detail, I should like to draw attention to the fact that the loss of eyes occurs in two stages.

The penultimate stage of eye degeneracy or anophthalmia, to adapt a medical term to an entomological usage, involves a condition in which the eyes are represented by minute round or oval, or convex white or colorless areas on the side of the head some distance behind the insertion of the antennae. Microscopic examination seems to reveal faint traces of ocelli in at least some instances. Among northwestern species such rudimentary eyes are present in three of our four species of *Anilloferonia* and in one, *Leptinillus*, of our three species of Leptinidae. Furthermore, similar rudimentary eyes are present in other blind Carabidae, as in certain eastern North American species of *Pseudanophthalmus* and certain European species of *Anophthalmus*, in certain eastern North American cavernicolous species of *Adelops* in the Catopidae, and in the middle Californian blind tenebrionid, *Eschatoporis nunenmacheri* Blaisdell.

The final or ultimate stage in the reduction of the eye is represented by the complete absence of any external trace of the eye structure. In the Northwest, one of our species of *Anilloferonia*, all of our *Catopocerus*, and two out of three of our species of Leptinidae belong to this category. It is a condition frequently present in both North American and European species of Trechinae in the family Carabidae, including species of both *Pseudanophthalmus* and *Anophthalmus* and is found in such European species of the cavernicolous Leptodirinae in the family Catopidae as I have been able to examine.

It is interesting to note that what I have termed the penultimate stage of anophthalmia, the stage involving the presence of rudimentary eyes, is present in at least five phylogenetically independent groups of beetles, and that in three of these five groups closely related forms have attained the ultimate stage of eyelessness in which all external signs of an eye are wanting. From this I suggest that it can be concluded that these two forms of anophthalmia are, from a phylogenetic point of view, closely related processes. Moreover, they are, perhaps, simply the extreme phase of a variation in the size of the compound eyes that related species in innumerable groups of beetles and other insects exhibit. The relative rarity of anophthalmia is, however, evidence that the conditions that permit such a condition to exist are similarly relatively uncommon.

The genus *Anilloferonia* was discovered in 1925 by the late Dr. Edwin C. Van Dyke on the east side of Mount Adams in the Cascade Mountains of Washington, at an altitude of about 4,000 feet, beneath an old log in the forest. Dr. Van Dyke told me later that he recognized immediately that he had made an interesting capture and made a strenuous but unsuccessful effort to secure additional specimens. A second specimen of what I consider to be the same species (*testacea* Van Dyke) was taken in a similar situation by Dr. P. J. Darlington, Jr., at an elevation of about 5,000 feet on Mt. Hood in Oregon, in the summer of 1927, and is now in the Museum of Comparative Zoology at Harvard.

The next and, to date, the most extensive find of *Anilloferonia* was made by that skillful and energetic collector, Mr. M. C. Lane, at Seaside, Oregon, in 1932 and 1933. When Mr. Lane returned from a collecting trip at Seaside in September, 1932, he found he had secured a single specimen of a blind Pterostichus-like carabid, and so in June of the following year he was back after more—and he found them! Here at sea level in the dense evergreen rain forest of Seaside in extreme northwestern Oregon Mr. Lane located the remnants of a long deserted lumber camp. In small rodent tunnels under twelve or fourteen inch logs sunk two-thirds of their diameter in the damp forest floor was taken a series of a dozen or fifteen specimens of the same rufotestaceous blind beetle. With it occurred two specimens of an undescribed species of the eyeless *Catopocerus* that I shall refer to later, two specimens of the scarabaeid *Aegialia montana* Brown, and an abundance of the burrowing *Pterostichus pumilis* Casey. Both of these last species are of the same rufotestaceous color as the *Anilloferonia*, but neither are blind, and the *Pterostichus* occurred at a lesser depth than the blind species.

Mr. Lane generously turned this choice material over to me for study. A close reading of Dr. Van Dyke's description revealed a number of minor features distinguishing the Seaside specimens from his, on the basis of which I described *Anilloferonia lanei*. Dr. Van Dyke later confirmed my judgment in regarding *lanei* as distinct, but, in comparison with the other two species of *Anilloferonia* that were discovered later, *testacea* and *lanei* are really very close and may eventually prove to be geographical races of a single species.

The remaining two species of *Anilloferonia* were found by me in the course of the preparation of Part I of my currently appearing work on *The Beetles of the Pacific Northwest*. The single specimen of *Anilloferonia rothi* was taken in August 1949 by Mr. Vincent Roth, another very successful collector of northwestern insects, at that time a graduate student in entomology at the Oregon State College in Corvallis. It was found on the slopes of Mary's Peak, a 4100 foot mountain about 15 miles southwest of Cornvallis, and one of the peaks that constitute the Coast Range at this point. This is, perhaps, the most specialized of the species; even the rudimentary eyes are wanting, and the form is more ventricose, the anterior width of the pronotum being greater than the width along the posterior margin.

The fourth and last of the species of *Anilloferonia* is represented by a unique female taken in July 1951 under a log at close to sea level at Coos Bay, Oregon, near the Pacific

Coast, about two-thirds of the way south along the coast of Oregon from the mouth of the Columbia River. It has given me pleasure to name it after another energetic and resourceful collector of Northwestern beetles, Mr. Borys Malkin, a graduate student in anthropology at the University of Washington. If the presence of a scutellar stria on the elytra can be interpreted as a primitive characteristic, *malkini* can perhaps be regarded as the most primitive of the known species of *Anilloferonia.*

Malkini completes the roll call of the known species of *Anilloferonia:* four species in all—two of them known from unique females, and one from two specimens—two of the species taken at sea level along the Oregon coast, one from the high Cascades on either side of the Columbia River, and one from one of the lesser peaks of the Oregon Coast Range. The genus constitutes one of the outstanding endemic elements in the Vancouverian fauna—the name that was used by Van Dyke for the fauna of the coastal area west of the Cascade Mountains and extending from southern and southeastern Alaska into northern California. The nearest affinities of the genus are with the subgenera *Hypherpes* and *Leptoferonia* of the genus *Pterostichus*, subgenera that are more or less confined to western North America and especially well developed in the Vancouverian region. There is good reason to suspect, accordingly, that *Anilloferonia* has evolved *in situ* from a *Hypherpes* or *Leptoferonia. Anilloferonia* is as yet very imperfectly known both taxonomically and ecologically. With two of its four species known from uniques, a third species from a pair of specimens, and the fourth from a short series from a single locality, two conclusions are suggested. One, the known specimens of three out of the four species are probably only "strays" from a deep subterranean habitat of some sort, which our collecting methods have so far proven inadequate to explore. The occurrence of *lanei* in rodent tunnels under deeply embedded twelve to fourteen inch logs is certainly suggestive, but this was, after all, in important measure, a man-made trap and may not indicate the whole story. My second conclusion is that there is every reason to suspect that additional species of *Anilloferonia* exist in the region. Some of these may be discovered by chance in the same way as those already known, but no extensive expansion in our knowledge of the group can be expected until the real habitat of the group has been discovered and methods have been developed for collecting in this situation.

Catopocerus is a genus of totally eyeless North American beetles. It was treated by Horn in 1880 as one of the six major divisions of his Silphidae, and I am treating it in my *Beetles of the Pacific Northwest* as one of the five major divisions or subfamilies of my Leiodidae. I have relied on the usually reduced eighth antennal segment to relate it to the Leiodidae, but it would be almost equally plausible to use the posteriorly open procoxal cavities to relate it to the Silphidae. However, the details of this classification do not especially concern us here.

The first species of the genus to be described was the *Catops cryptophagoides* of Mannerheim from southeastern Alaska in 1852. *Catopocerus* goes back to a name proposed by Motschoulsky in 1869, and *Pinodytes Horn*, *Homaeosoma* Austin, and *Typhloleiodes* Hatch are apparently synonyms. When I began the study of this genus for inclusion in Part II of *The Beetles of Pacific Northwest* the situation as regards it was somewhat similar to that I have just described for *Anilloferonia*. There were a scattered few specimens of *Catopocerus cryptophagoides* without habitat data. There were the two specimens that Mr. Lane had taken at Seaside, Oregon, with *Anilloferonia lanei*, which I had described as *Typholeiodes subterraneous*, genus and species new, but which restudy now convinced me were cogneneric with *Catopocerus*. And there was a third, an undescribed species that Dr. I. M. Newell had taken at Coos Bay, Oregon.

And then last year we began a very belated use of the Berlese funnel. Mr. Vincent Roth, then of the Oregon Department of Agriculture at Salem, and his assistant, Mr. Joseph Capizzi, ran an extensive series of samples from various localities in western Oregon; and, at my direction, Dr. Dennis Boddy, at that time my research assistant at the University of Washington, ran a similar series from the vicinity of Seattle. In our Seattle samples, variously from leaf litter, pine litter, cedar litter, alder litter, humus and moss, specimens of *Catopocerus* literally "rained down", which was gratifying even though they all seemed to belong to the single species, *cryptophagoides* Mannerheim. The unmounted Berlese samples from western Oregon that Mr. Roth very generously sent me for study similarly contained their share of *cryptohagoides*, but likewise had representatives of some seven other species, two of them identical with the Seaside and Coos Bay species I had previously seen and five of them additional and undescribed species. Rotting wood duff, Douglas fir duff, moss and forest duff indicate the sorts of material from which these Oregon samples came. Finally, from the coastal region of northern and middle California, which is a direct continuation of the coastal region farther north, there are two further species of Catopocerus known, the *pusio* of Horn and an undescribed species extensively represented in three Berlese samples from Mendocino, that I owe to the kindness of Mr. Jaques Helfer.

We thus find the Vancouverian Region from southeastern Alaska to middle California populated by 10 species of this interesting anophthalmous genus. Moreover, with the exception of a single species represented by a unique specimen, the species are represented in our collection by series of specimens that range in number from a dozen or fifteen up to more than a hundred. Again many of the species are well characterized by easily appreciated characters. Prominent differences in the body form, in the relative size and shape of antennal segments. and in elytral sculpture are present. One species has the apex of the metatibia in the male conspicuously arcuate. There are, however, three species in Oregon, one of which is the common *cryptophagoides*, that so far I must separate primarily on the basis of male genitalia. Moreover, the nine species that are represented by more than one specimen have all been taken on more than one occasion, mostly in several localities. Finally, all the species have been taken with other species of the same genus, and there were five samples that contained three different species each and not always the same three.

Outside the Vancouverian Region, one of the undescribed species of *Catopocerus* from western Oregon is likewise hnown from Kooskooskie in the Blue Mountains of southeastern Washington and from Julietta in northern Idaho. Finally, in northeastern North America, *hamiltoni* Horn occurs near Pittsburgh, Pennsylvania, and *ulkei* Brown in the District of Columbia. Hamilton (1897) reported *hamiltoni* as being gregarious in woody, hilly, uncultivated places in subterranean or semi-subterranean situations, the adults sometimes occurring under bark of logs, and being found oftener in winter than in summer. The adults apparently feed on dead larvae and pupae of other insects. On the basis of present knowledge, the genus is thus a preponderantly Vancouverian genus with scattered representation elsewhere on the continent. However, our northwestern experience indicates that specimens are very infrequently taken without Berlese funnel sampling. Accordingly, until such collecting has been done more widely, attempts to interpret the distribution of the genus is probably premature.

The third group of blind beetles in the fauna of the Pacific Northwest with which I am personally familiar includes single species in each of the three genera: *Leptinillus*, *Leptinus*, and *Platypsyllus*, which, from the point of view of the northwest fauna, I consider as the family Leptinidae. They have quite a different status from the two groups I have been discussing. In the first place, none of our species can in any sense be regarded as peculiar or particularly characteristic of any portion of the northwestern fauna, but occur there only as this portion of the continent has been open to population from adjacent areas. The northwestern species are all of them well known and I have nothing strikingly new to present in regard to them. In the second place, none of these beetles are ground inhabiting burrowers, like *Anilloferonia* and *Catopocerus*, but are ectoparasites on mammals. They have accordingly, presumably, lost their eyes by a different route and in response to a different set of environmental factors.

The most easily obtainable of our species is the completely blind *Platypsyllus castoris* of Ritsema. It is peculiar enough and on all counts one of the most extraordinary of beetles, so anomalous in fact that it was first believed to be a distinct order of Insects by Westwood in 1869 which he called the Acheiroptera. But these are matters that have been abundantly discussed in the past. The beetles are not to be found, of course, except on living or recently dead beaver. I have seen specimens from four localities in Washington and one in British Columbia and my most extensive series, over 50 specimens of adults and numerous larvae, came from a freshly drowned beaver that my son had caught by mistake in a trap north of Seattle. The specimens were secured in the fur before turning the beaver over to the State Museum.

The other two species of our Leptinidae are rare. I have seen 'a single series of *Leptinillus validus* Horn from Bowron Lake in the Cariboo Mountains in the interior of British Columbia. This species has minute rudimentary white eyes, it was described from the Hudson Bay country, and, like *Platypsyllus*, is parasitic on the beaver. A second species has been described from the mountain beaver, *Aplodonta rufa*, in northern California, by G. F. Ferris (1918). The mountain beaver belongs to a different family of rodents than does the true beaver and is not closely related to it either in structure or habits.

The third species of Northwestern Leptinidae is the completely blind *Leptinus americanus* LeC. The North American populations have usually been considered cospecific with the European *testaceus* Muller, but Werner and Edwards adduced evidence in 1948 for regarding the Nearctic form as distinct. They are ectoparasites of field mice, moles, and shrews and are very rarely collected. I have single specimens from Skokomish, Washington, and Lincoln County, and near Coquille, Oregon, the latter taken from a Townsend mole.

I conclude my discussion of these ectoparasitic beetles with the suggestion that the apparent rarity of some of the species is perhaps due to the failure of mammalogists and other trappers of small mammals to examine their recently dead specimens with sufficient care to discover the beetles. Perhaps beetle collectors should trap their own mammals!

Every student of blind beetles must be intrigued afresh with the problem presented by the evolutionary loss of eyes. The genetics of such loss apparently does not present too much difficulty. In *Drosophila* it is known that the difference of a single gene can account for the complete absence of eyes. Furthermore, under laboratory conditions, most of the mutations that occur in any stock of organisms have degenerative or simplifying effects on the structure of the body. Such degenerative genes are, of course, being continually eliminated by natural selection by organisms in nature. There is no difficulty, then, in understanding how such a degenerative change as that represented by anophthalmia might arise in a population of organisms that found itself in an environment in which eyes are no longer of any use. There is no doubt of the existence of a causal relationship between such an environment and a loss of eyes. The difficulty is to see exactly how such a causal relationship works itself out. The Lamarckian explanation is definitely not available; the overwhelming evidence of seventy-five years of experimental breeding is against the inherited effect of disuse. Moreover, mathematical analysis shows that a mutation of merely neutral value does not establish itself completely in a population. Accordingly we are left with the necessity to conclude that there must be some selective advantage to the loss or extreme reduction of eyes in habitats where they have ceased to be of use. Can it be that the energy involved in developing an eye is of sufficient moment so that an organism that is relieved of this necessity has an advantage over an organism that is not so relieved, provided that the organism lives in a habitat in which eyes are of no use? And what of the rudimentary eyes to which I have been calling attention? Can it be that there are situations in which they convey an advantage that is superior both to the possession of fully developed eyes and to the complete absence of eyes? On these queries I conclude.

REFERENCES

Ferris, G. H. 1916. An apparently new species of *Leptinillus* (Coleoptera, Leptinidae). *Canadian Ent.* 50: 125–128.

Hamilton, John. 1897. *Pinodytes hamiltoni* and *Anthicus formicarius*. *Ent. News* 8: 34–35.

Hatch, Melville H. 1953. The beetles of the Pacific Northwest. Part I: Introduction and Adephaga. *Univ. Wash. Publ. in Biol.* 16: 340 pp. 38 plates.

Hatch, Melville H. 1957. The beetles of the Pacific Northwest. Part II: Staphyliniformia. *Univ. Wash. Publ. in Biol.* 16: 384 pp. 38 plates.

Wickham, H. F. 1890. Remarks on some western Tenebrionidae. *Ent. Americana* 6:83–88.

Sur les Relations entre les Buprestides de la Région paléarctique et néarctique

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RÉSUMÉ

Le nombre actuel des espèces de Buprestides est d'environ 16,000 (11,391 en 1937) et serait approximativement 35,000 si l'on y incluait toutes les variétés. De ce nombre, 725 espèces sont néarctiques et 2,200 paléarctiques. La faune paléarctique est donc plus de trois fois plus nombreuse que la faune néarctique. En étudiant la faune holarctique des Buprestides, on s'aperçoit que les espèces néarctiques sont généralement beaucoup moins variables et plus stables que les espèces paléarctiques, principalement dans la partie occidentale de cette zone, où quelques genres tels que Julodis, Ptosima, Anthaxia, Agrilus, *ont un nombre considérable de variétés, tandis que les espèces de ces mêmes genres varient très peu en Amérique. Un bon exemple est la comparaison entre* Ptosima gibicollis *Say d'Amérique et* undecimmaculata Herbst *d'Europe, dont on connaît plus de 150 aberrations bien distinctes. Une variation considérable se rencontre chez l'espèce méditerranéenne* Julodis onopordi *L. qui comprend 12 races géographiques et plus de 45 formes se comportant parfois comme espèces distinctes. Par exemple, on rencontre aux environs d'Athènes les deux races* J. o. pilosa *F. et* J. o. egrenbergi Cast. *du nord sans y trouver de formes intermédiaires. On peut expliquer cette stabilité relative des espèces néarctiques et la variabilité considérable des espèces européennes et du bassin de la Méditerrannée par le caractère différent des périodes glaciaires et interglaciaires en Amérique du nord. Sur ce continent, les montagnes, généralement dirigées du nord au sud n'ont pas formé de barrière contrôlant la fluctuation et la réintroduction des espèces après les bouleversements climatiques. En Europe, au contraire, les chaînes de montagnes forment des barrières transversales se dirigeant de l'est à l'ouest, ce qui a provoqué, à travers les âges, durant les périodes glaciaires et interglaciaires, des changements climatiques beaucoup plus considérables qu'en Amérique du nord. Ceci a provoqué une variation beaucoup plus complexe même chez les espèces qui ont réagi aux variations déterminées par les facteurs du milieu. Il est curieux d'observer que les espèces reliques des Buprestides de l'Europe, telles que* Anthaxia türki Ganglb., Cypriacis splendens *F.,* Dicerca herbsti *Kiesenw., sont très voisines des quelques espèces néarctiques de la côte du Pacifique et non de l'Atlantique.*

Ayant eu la possibilité, pendant les cinquante ans derniers, de voir un immense nombre des Buprestides paléarctiques ainsi que d'étudier de grandes séries de Buprestides néarctiques, je pouvais très souvent constater le divers degré de variation et de variabilité générale des espèces de ces deux faunes. Le nombre des espèces de Buprestides actuellement connus est environ 16,000; en 1937, quand j'ai fini mon Catalogue des Buprestides du Monde, 11391. Le nombre actuel des espèces, sous-espèces, variétés et aberrations remonte aujourd'hui aux quelques 35,000 formes. De ce nombre 725 espèces sont néarctiques et 2,200 paléarctiques. Alors le nombre des espèces néarctiques ne fait pas que moins qu'un tiers des paléarctiques. Parmi les paléarctes ce sont surtout les espèces de l'Europe, du Bassin de la Méditerrannée et de la Lévante, qui sont des plus variables, tandis que les espèces voisines, vivantes sur les mêmes largeurs géographiques en Amérique montrent une variabilité beaucoup moindre. Une comparaison de treize sous-familles (tribus, erronneusement chez Kerremans) de Buprestides donne, dans les deux régions, les dates suivantes (nombre des espèces connues).

I.	Sous-famille Julodinae: néarct.	0 ,	paléarct. 51
II.	Sous-famille Acmaeoderinae	163	271
III.	Sous-famille Schizopnae	7	0
IV.	Sous-famille Thryncopyginae	5	0
V.	Sous-famille Chrysochroinae	0	22
VI.	Sous-famille Chalcophorinae	69	78
VII.	Sous-famille Sphenopterinae	0	668
VIII.	Sous-famille Bubastinae	0	1
IX.	Sous-famille Buprestinae	177	358

X.	Sous-famille Chrysobothrinae	129	51
XI.	Sous-famille Stigmoderinae	0	0
XII.	Sous-famille Agrilinae	172	700
XIII.	Sous-famille Mastogeninae	5	0
		725	2200

De sous-familles précitées les Julodinae manquent en Amérique absolument; de la sous-famille Acmaeoderinae le tribus Julodimorphini manque dans les deux faunes; le tribus Polycestini a seulement un genre commun aux deux faunes: *Polycesta* Solier. Ce sont formes anciennes et peu variables. De plus, en Amérique existe un genre bien péculier, *Chrysophana* Le C., spécial pour la faune néarctique, tandis qu'en Ancien Monde sont connus encore les genres *Pseudocastalia* Kraatz et *Strigoptera* Dej. *Castelia* C. et G., avec 7 espèces paléarctiques et un genre monotypique, inconnu à moi et d'ailleurs très suspecte *Thurntaxisia* Schatzm. (*Alexandri* Schatzm.). Tribus Ptosimini a pour les deux faunes un seul genre commun, *Ptosima* Solier, avec trois espèces en Amérique et trois paléarctiques. La plus commune d'espèces américaines est *Ptosima gibbicollis* Say avec une seule variété, tandis que *Ptosima undecimmaculata* Hbst. de l'Europe en a plus que 150, dont quelques très remarquables. Même en Europe centrale, en Tchécoslovaquie méridionale, surtout en Slovaquie cette espèce varie énormément. En Amérique du Nord il y a encore une espèce du genre *Tyndaris* J. Thomson—ce genre étant néotropique—et 12 espèces du genre péculier et très caractéristique pour les régions arides du Texas, Arizona, Nevada, et Californie, *Paratyndaris* Fisher. A l'autre côté, dans la région paléarctique il y a deux genres, *Polyctesis* Mars., 3 esp., et *Paratrachys* E. Saunders, 3 esp. Les autres espèces de ces genres appartiennent à la faune orientale. Le tribus Acmaeoderini est représenté dans les deux faunes, dans la faune néarctique par 140, paléarctique 250 espèces. Tandis que les nombreuses espèces américaines varient assez faiblement, quelques espèces paléarctiques sont extrêmement variables et forment beaucoup de races géographiques bien distinctes. Une des plus communes espèces de l'Europe méridionale est *A. bipunctata* A. Oliv. Elle varie énormément, tandis qu'une espèce bien semblable américaine *A. tubulus* F. varie bien faiblement. Sous-famille Schizopinae est très caractéristique pour l'Amérique du Nord et tout spécialement pour Californie. *M. Théry* l'a divisé en deux, en séparant les Dystaxiines par les Schizopines, mais je ne suis pas de son avis. On a, de même, voulu séparer cette sous-famille par les Buprestides en la considérant comme une partie de la famille de Dascillidae, mais je pense, que cette opinion n'est pas justifiée et, en cet égard je suis de même avis avec *M. R. A. Crowson*, l'auteur de "Classification naturelle des Coléoptères", récemment parue. De même IV. sous-famille Thrincopyginae est exclusivement américaine. V. Sous-famille Chrysochroinae est d'origine orientale et africaine et les espèces paléarctiques appartiennent aux genres d'origine exotique. En Amérique cette sous-famille manque absolument. VI. Sous-famille Chalcophorinae a un seul genre commun aux deux zones, *Chalcophora* Solier, avec 14 espèces américaines et 10 paléarctiques. Le genre *Texania* Casey, avec 7 espèces américaines est voisin au genre japonnais *Nipponobuprestis* Obenberger, 2 espèces. Typicalement paléarctiques sont les genres *Lamprocheila* Obenb., une espèce chinoise, *Stigmatophorella* Obenberger, 4 espèces, *Chalcophorella* Kerremans, 2 espèces, et *Rossiella* Obenberger, une espèce. Dans la région paléarctique existent encore deux espèces du genre *Iridotaenia* H. Deyrolle et deux du genre *Chrysodema* Cast. et Gory—les deux genres étant d'origine orientale. L'Amérique boréale a quatre genres caractéristiques: *Agaeocera* Waterh., une espèce, et trois genres très rapprochés, d'un caractère spécial, qui remplacent vraisemblablement les *Sphénoptères* paléarctiques, c'est-à-dire: *Hippomelas* Casey, *Gyascutus* LeConte et *Stictocera* Casey. Leur systématique n'est pas encore satisfaisante. Ils contiennent 39 espèces. Tous les genres précités appartiennent au tribus *Chalcophorini*. Dans le deuxième tribus, *Psilopterini*, appartient le grand genre *Psiloptera* Solier, représenté dans les deux régions par le sous-genre *Lampetis* Spinola, avec 11 espèces paléarctiques et 8 néarctiques. Les espèces néarctiques sont d'une forme un peu aberrante et M. Casey a créé pour eux le nom générique *Spinthoptera* Casey, qui je ne trouve pas assez justifié. En région paléarctique proviennent encore deux espèces du sous-genre *Damarsila* J. Thomson, qui est représenté par beaucoup d'espèces en région éthiopienne. La région paléarctique a, dans ce tribus, 4 genres très caractéristiques et exclusivement paléarctiques: *Capnodis* Eschscholtz, 17 espèces, *Cyphosoma* Mannerheim, 10 espèces, *Perotis* Spinola, 10 espèces, et *Latipalpis* Solier, 4 espèces. VII. Sous-famille Sphenopterinae est surtout paléarctique: sous-genres *Sphenoptera* s. str., *Deudora* B. Jak., *Rhaphidochila* B. Jak., *Chrysoblemma* B. Jak., *Chiloblemma* Obenberger, *Chilostetha* B. Jak. entièrement, sous-genres *Hoplistura* B. Jak. et *Tropeonpeltis* B. Jak. pour une partie d'espèces étant paléarctiques. Ce sont les espèces des steppes arides, très difficiles et, pour la majeure partie, fort rares. Les deux sous-genres derniers ont un nombre très grand surtout en Afrique et en Asie continentales. Dans la région paléarctique cette sous-famille, qui manque absolument en Amérique, est représentée par 668 espèces. Tribus VIII. Bubastini, dont la plupart d'espèces est d'origine australienne est représentée dans la région paléarctique (Algérie) par une seule espèce du genre *Paratassa* Marseul. Elle manque absolument en Amérique, sinon le genre *Ampheremus* Fall, incomplètement décrit, ne se devrait rapporter ici. La sous-famille Buprestinae, tribus Dicercini, est représentée par deux genres dans les deux régions: *Dicerca* Eschsch., 63 espèces néarctiques, 17 paléarctiques, et *Poecilonota* Eschsch., 10 néarct., 10 pal. Genre caractéristique américain: *Cinyra* C. et G., 9 espèces. Dans la région paléarctique existent en plus: genre *Lampra* Sol., 61 esp., *Cardiaspis* E. Sd., 1 esp., et *Touzalinia* Théry, 1 esp. de Chine. Il est fort intéréssant que l'espèce relicte européenne presqu'extincte, *Dicerca herbsti* Ksw. ressemble beaucoup aux quelques espèces de Californie. Tribus Buprestini est représenté par deux genres dans les deux régions: *Buprestis* L. avec 23 esp. paléarctiques et 21 néarctiques, dont trois du sous-genre *Stereosa* Casey. *Stereosa apricans* Hbst. était trouvée aussi dans un port de l'Espagne. Le genre *Cypriacis* Casey est représenté dans la région néarctique par 13, dans la région paléarctique par 6 espèces. Le rarissime et vraisemblablement extinct *C. splendens* F. de l'Europe centrale et méridionale est bien proche aux certaines espèces de la côte pacifique de l'Amérique du Nord. Dans la région paléarctique il y a encore le genre *Eurythyrea* Lacordaire, 7 espèces, et *Yamina* Kerr., 3 espèces, exclusivement paléarctiques. On range dans ce tribus provisoirement aussi le genre douteux *Ampheremus* Fall. Dans le tribus *Anthaxiini* il y a deux genres communs aux deux régions: *Melanophila* Eschsch. (*Phaenoips* auct.) avec 20 espèces (*M. acuminata* Pallas holarctique) américaines de variabilité modeste et 21 paléarctiques, dont *M. picta* Pallas avec une variabilité énorme, et *Anthaxia* Eschacholtz, avec 205 espèces paléarctiques et 30 américaines—on y en trouvera certainement plusieurs. Exclusivement américain est le genre *Agrilaxia* Kerr., 4 espèces, exclusivement paléarctique, *Kisanthobia* Mars., 1 espèce. De plus, *Coomaniella* Bourgoin, 2 espèces, et *Chalcogenia* Mars., 4 espèces pal. X. Sous-famille Chrysobothrinae, tribus Chrysobothrini a seulement le genre *Chrysobothris* Eschscholtz avec 121 espèces néarctiques et 47 paléarctiques. Tribus Actenodini est représenté seulement dans la région néarctique par 8 espèces du genre *Actenodes* Lac. XII. Sous-famille Agrilinae a un seul genre commun aux deux régions: *Agrilus* Stephens, 145 espèces néarct., 324 paléarct. Genres exlusivement néarctiques: *Eupristocerus* H.D., 1 esp., *Paragrilus* E. Sd., 3 esp., et *Engyaulus* Wat., 1 esp. Le plus remarquable genre paléarctique est *Clema* Sem. de l'Asie centrale, dont les plus voisines formes sont en Australie. Les autres genres paléarctiques: *Pseudoclema* Théry, 1 esp., *Discoderoides* Théry, 1 esp., *Cryptodactylus* Deyr., 3 esp., *Toxoscelus* H. Deyr., 4 esp., *Metasambus* Kerr., 1 esp., *Coraebus* C. et G., 75 esp., *Meliboeus* H. D., 68 esp., *Sambus* H. D., 20 esp., *Pseudagrilus* Cast., 1 esp., *Coraegrilus* Frm., 1 esp., *Coraebina* Obenb., 7 esp., *Paracylindromorphus* Théry, 25 esp., *Cantonius* Théry, 3 esp., et *Cylindromorphus* Théry, 19 esp. Dans le tribus Trachydini en Amérique boréale: *Brachys* Sol., 7 esp., *Taphrocorus* Sol., 10 esp., *Pachyschelus* Sol., 5 esp.—paléarctiques: *Endelus* H. Deyr., 9 esp., *Aphanisticus* Latr., 16 esp., *Trachys* F., 116 esp., *Janthe* Mars., 2 esp. Le genre neotropique *Pachyschelus* a en Amérique bor. 5 espèces. Une espèce est connue de Chine. Le sous-tribus *Mastogenina* est représenté seulement dans la région néarctique: *Mastogenius* Sol., 4 espèces, *Trigenogya* Ch. Schaeff., 1 esp.

La relativement faible variabilité des espèces de l'Amérique du Nord et la variabilité, parfois étonnante et énorme de diverses espèces paléarctiques, surtout de l'Europe et du Bassin de la Méditerrannée est bien explicable par écoulement différent des périodes glaciaires et interglaciaires en Amérique et en Europe. La direction générale des montagnes de l'Amérique du Nord est du Nord au Sud, alors les "lignes de retraite" vers le sud étaient pour la faune plus commodes et plus faciles, tandis qu'en Europe, où la plupart des montagnes a une direction de l'Ouest à l'Est ces montagnes faisaient un arrêt, une barrière, ce qui a provoqué certainement les bouleversements plus compliqués et changements du climat plus profonds qu'en Amérique et tout cet ensemble des influences climatiques dans le progrès et les récessions des temps glaciaires et interglaciaires a pour les faunules les conséquences différentes de celles en Amérique. En Amérique la faune pouvait plus facilement évacuer le terrain perdu et le récupérer dans une époque plus favorable, tandis qu'en Europe la faune du terrain envahi par les influences glaciaires était soit éliminée totalement, ne pouvant pas traverser les barrières de montagnes, ou elle se devait accommoder plus rapidement aux conditions nouvelles, ce qui a provoqué une variation intensive, distincte encore maintenant dans les variétés nombreuses. La probabilité de cette hypothèse est fortifiée par le nombre très grand des Coléoptères terricoles en Europe, surtout méridionale et le petit nombre relatif de ces espèces en Amérique et surtout aussi le nombre très grand des espèces hypogées et aveugles, speléophiles de l'Europe méridionale. Quelques espèces, comme par ex. le grand *Julodia onopordi* L. varient énormément; cette espèce a autour de la mer Méditerrannéenne 12 races géographiques générales avec quelques 45 formes inférieures et quelques entre ces races ont a peu près un caractère d'une espèce. *J. onopordi ssp. pilosa* F., venant de Sud-Est, rencontre dans les environs des Athenes, en Grèce, une autre race, *J. onopordi ssp. Ehrenbergi* Cast. sans y pouvoir produire des formes intermédiaires. L'histoire géologique et situation géographique jouent alors un rôle fort important dans la formation des catégories inférieures d'une espèce et on doit toujours respecter ces facteurs, quand on veut connaître plus profondément la variabilité des espèces—*et connaître une espèce, c'est connaître sa variabilité.*

The Two Larval Forms of *Meloë violaceus* Marsh., and Species Distinguishable only in the Early Stages

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ABSTRACT

The problem of the pale and dark forms of the first-stage larva of Meloë violaceus *was recognized and discussed by the late K. G. Blair (1942), who came to the conclusion that either two very similar British species must be concealed under the name* M. violaceus, *or that two geographical races, recognizable only in the larval stage, must exist in that country. As the pale form, like the dark one, has been found in Central Europe (Emden, 1943) and Suffolk, both forms seem to co-exist over a large area and are unlikely to be subspecies. The discovery of various structural characters (slightly smaller size; stouter femora, which are also shorter in proportion to the head-width; shorter tibiae; a somewhat differently shaped ninth tergite; and a shorter head with a more V-like frontal suture in the pale form, as compared with the more lyre-shaped sutures of the dark form) now confirms the view that two closely related species are concerned, recognizable only in the larval stage. Similar cases affecting larvae or pupae are known in* Trachys griseofasciata *Saund. (Buprestidae),* Orthocladius rubicundus *Meig. (Chironomidae),* Culicoides nubeculosus *Meig. (Ceratopogonidae),* Anopheles umbrosus *Theo. (Culicidae), the genus* Tripteroides *(Culicidae) and various Simuliidae. As egg, larva, pupa, and adult combine to form the species, of which the characters are inheritable only by the sexual propagation of the adult, there is no question of larval or pupal "species" not existing in the adult, and distinguishing characters for the latter will probably be found ultimately. However, the cases discussed and other examples show that the amplitude of interspecific variation is not necessarily greatest in the adult but may be more conspicuous in some early stage.*

Newport (1851) was the first to describe the first-stage larva of *Meloë violaceus* Marsh. Cros (1934) proved that this yellow larva can only belong to the same species as Kirby's blackish "*Pediculus melittae*", and he explained the difference of coloration by assuming that Newport described freshly hatched specimens, and that these would have become dark later, if they had been kept alive longer. In 1942 K. G. Blair reviewed the problem, having bred the dark larva from the eggs of a female *M. violaceus* and having found that they obtain the dark coloration within 24 hours of hatching. These larvae hatched only at the end of September after an incubation of about three months, whereas in Newport's experiments only three weeks, one-fourth the time, passed between oviposition and hatching. Moreover, it was clear from Blair's breeding experiment and captured material that the black larval form must hibernate before entering the nest of the host. He, therefore, concluded that there must be either two very similar British species identified as *M. violaceus* or two subspecies, one of which had so far only been found in E. Kent (by Newport).

However, it is obvious that the pale form is much more widely distributed, as Cros (1929) had seen it from Innsbruck and Vienna, and as I had received it in 1932 from Berlin (bred by the late Eugène Rey). I have since obtained from Mr. V. W. Fowler two specimens found at Woodbridge, Suffolk. Thus, the pale form is probably as widely distributed as the dark form, which I have seen from Devonshire, Somerset, Middlesex, Norfolk, Hamburg and Dresden (Emden, 1943) and which Cros (1929) records from Cassel and the Ardennes. It is thus not likely that the two forms are different geographical races. The biological difference stressed by Blair also is not borne out by the observations now available and is apparently only due to seasonal factors, for like Blair's dark larvae the pale larvae reared by Rey had hatched late in the year after an incubation of about three months (eggs deposited 6. VI. 32, larvae hatched 26. VIII.-6. IX. 32). From these various observations it appears practically certain that the two forms are not subspecies but either insignificant larval modifications or good species (Emden, 1943).

It was desirable, therefore, to compare the forms carefully for structural differences. Already in Blair's key (1942, p. 115) the length of the dark larval form is stated to be 2.4 mm. against 2.2 mm. for the pale specimens. In itself this difference is hardly significant, but it is in accordance with the figures for the head-width contained in my paper (1943, p. 222). These are 0.35–0.39–0.41 mm. for the dark and 0.34–0.36–0.37 mm. for the pale larvae (dry material disregarded.) More conspicuous are the characters revealed by camera lucida drawings, which show that in the dark form the head, notably the frontale, is longer (Fig. 1), the frontal sutures define a more lyre-shaped sclerite (in the pale form, a more V-shaped one), the ligula (Fig. 2, *l*) is shallowly emarginate in the dark, but evenly convex in the pale form, the cardo (Fig. 2, *c*) in the pale form is much more reduced, and the setula of the cardo is situated on the membrane. The legs appear particularly strikingly different, those of the dark larva being much longer and more slender (Fig. 3). Even more than the drawings, measurements (Table I) bring out decisive differences. These are found in the length of the femora (but not their width), in their stoutness (the length of the dark form equalling 2.6 times the width, that of the pale form hardly twice), in the length of the tibiae (in the dark form practically as long as the head-width, in the pale form only seven-tenths that width), the length of the frontale and of the whole head. The relative width of the prothorax and other segments offer minor characters as shown in the table. The total of these differences is such that there can be little doubt that the forms represent two good species strikingly differing as larvae but so far indistinguishable as adults.

TABLE I. Measurements in Per Cent of Head-Width.

Part of body		Dark larval form				Pale larval form			t test
	n	minimum	mean	maximum	n	minimum	mean	maximum	
Front femur: length	8	80.0	81.6	83.0	10	55.7	60.6	64.3	20.24
width	8	28.6	32.0	34.3	7	28.6	31.3	34.3	0.699
					10	28.6	32.2	34.3	0.206
width/length	8	2.41	2.56	2.80	7	1.87	1.96	2.10	9.43
					10	1.62	1.89	2.10	10.37
Front tibia: length	8	94.2	97.5	100.0	10	64.3	69.8	74.3	21.03
Frontale: length	4	60.0	62.0	65.0	5	48.6	52.9	54.3	5.817
Head: length	4	80.0	84.8	90.0	5	74.2	75.1	77.1	5.062
Pronotum: length	4	77.2	78.6	81.4	5	65.7	70.8	80.0	2.40
width	4	110.0	112.8	116.0	5	100.0	112.8	126.0	0.00
width/length	4	1.38	1.45	1.50	5	1.52	1.59	1.63	4.325
Abdominal segment 5: length	4	35.7	37.85	40.0	5	28.6	32.86	37.1	3.27
width	4	110.0	112.5	114.0	5	101.0	114.0	129.0	0.249
width/length	4	2.80	2.97	3.17	5	2.96	3.46	3.64	3.08
Abdominal segment 9: length	4	42.8	44.1	45.2	5	37.1	41.1	45.7	1.530
width	4	61.4	64.25	67.1	5	57.2	62.58	68.6	0.624
width/length	4	1.36	1.46	1.57	5	1.38	1.53	1.60	1.169

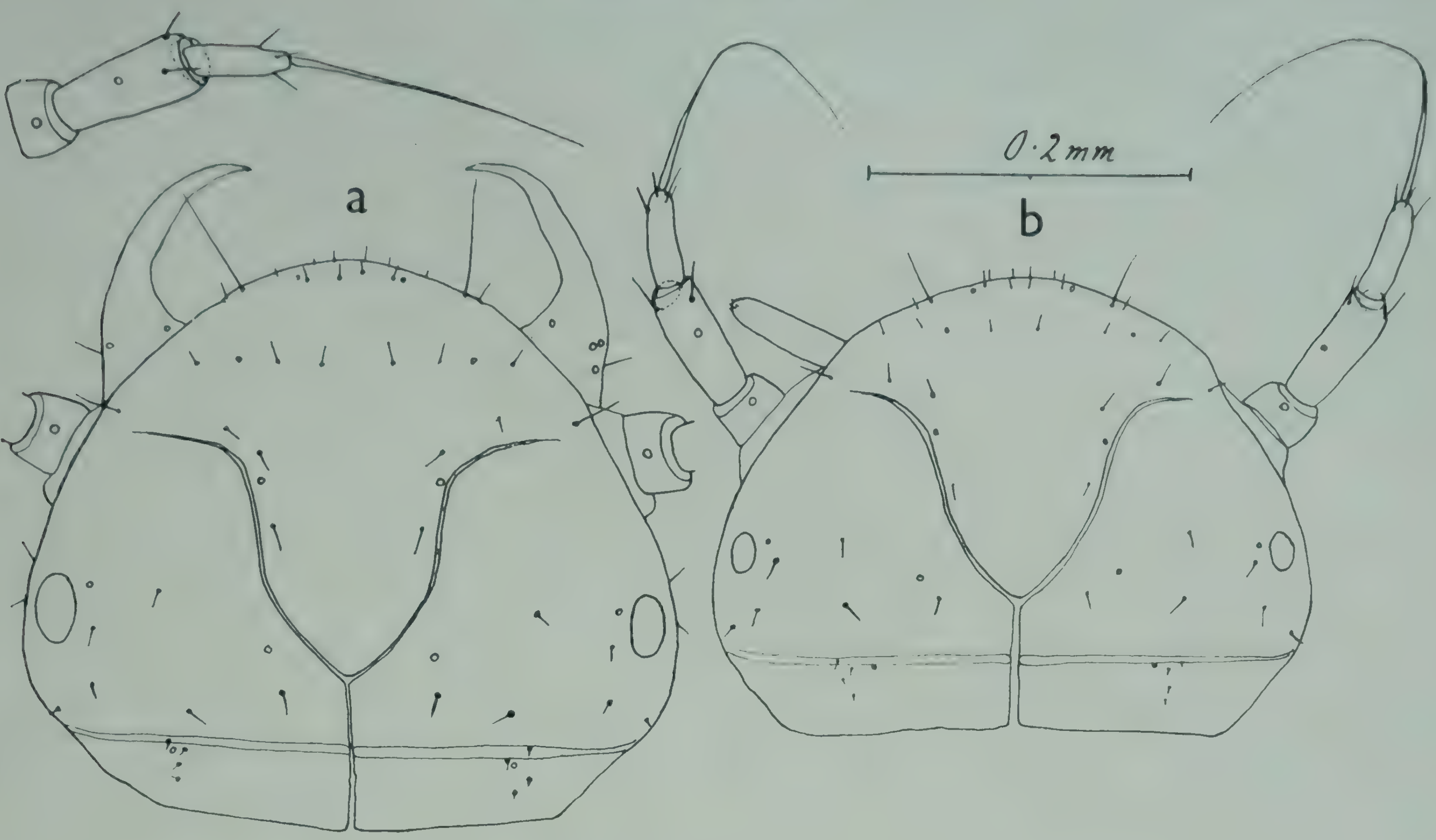
n: number of observations. For width and width/length of the front femur of the pale form, two values are given; in the upper line, three legs in which the femur lies beneath the body on the slide have been disregarded.

The figures have been drawn with a camera lucida and a microscope with Winkel eyepiece 2 and Watson objective 30 x. The scale represents 0.2 mm.

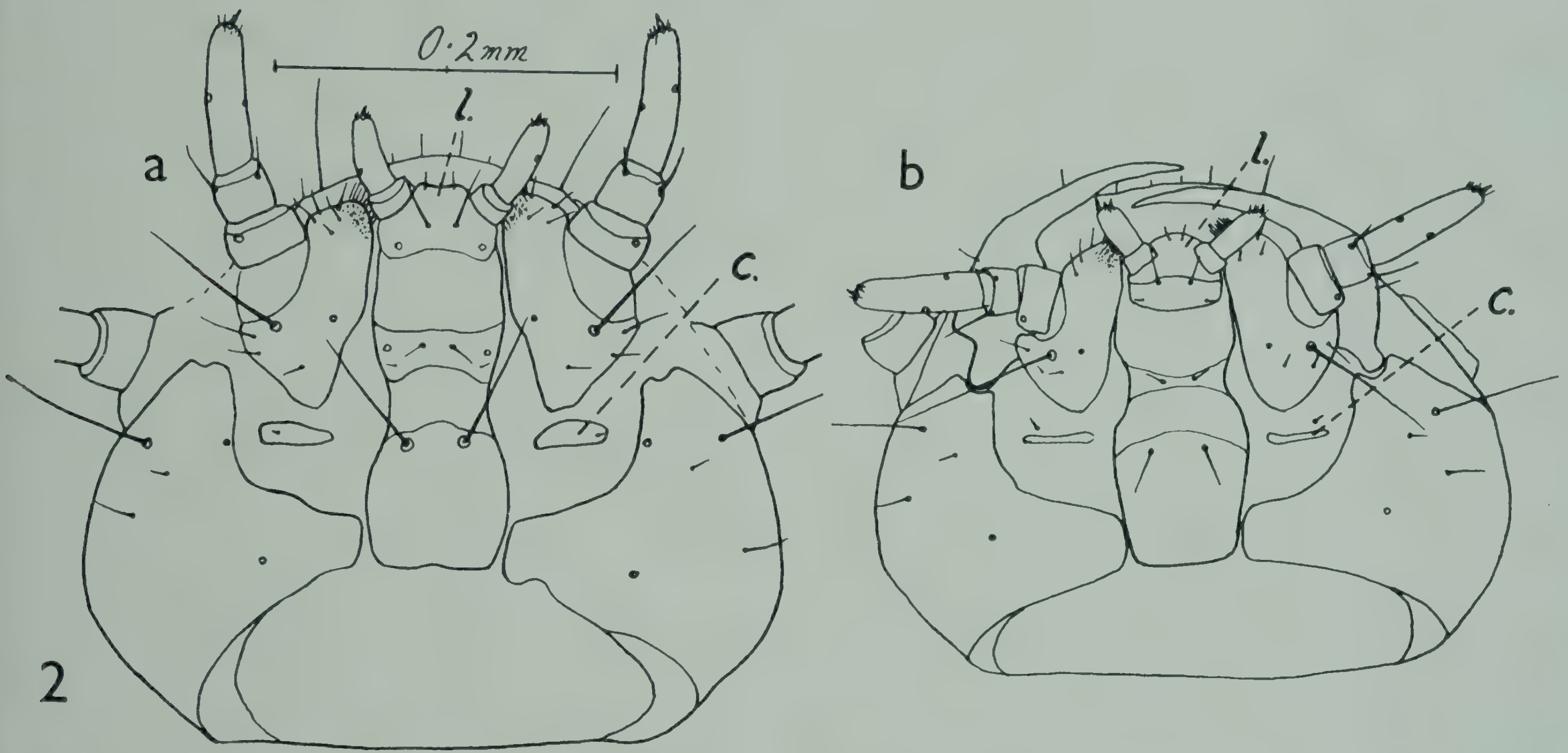
Fig. 1. Dorsal view of head; a, dark form; b, pale form.

Fig. 2. Ventral view of head; a, dark form; b, pale form. *c*, cardo; *l*, ligula.

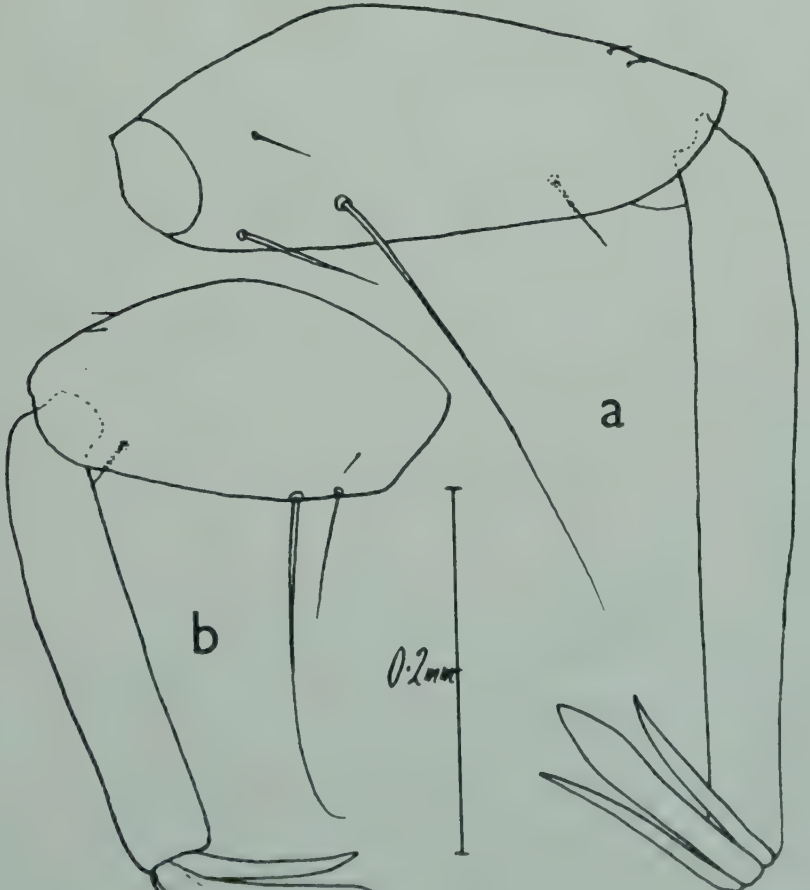
Fig. 3. Femur, tibia, and claw of front leg; a, dark form; b, pale form.



1


0·2mm
a
l.
c.
b
l.
c.

2



3

In most groups of insects the adults are more differentiated than the larvae and other early stages, and the widely-held view is probably correct that as a rule the early stages of closely related species differ less from each other than the adults. Nevertheless, to some extent, this opinion is due to the fact that the characters and classification of the early stages are much less explored than those of the adults. In consequence of this, the relevant characters are less easily spotted, as only a repeated study of systematic groups sharpens the eye of the student for differences. As painstaking research on the early stage of insects has become more general and more intensive, the number of cases has increased in which different species have first been noticed in an early stage. In the Japanese buprestid *Trachys griseofasciata* Saund., Yano (1952) found two types of eggs, larvae, and pupae living on different genera of plants, so that there can be little doubt that two species are involved, the adults of which are at present indistinguishable. In studying the larvae of Indian Geometridae, Singh (1953) discovered a considerable number of cases in which more or less clearly distinct larvae had yielded apparently identical adults. Among the best-studied groups of insect larvae are those of Culicidae, Ceratopogonidae, and some other Nematocera, and it is only natural that several similar cases are known in these families, e.g., in *Tripteroides* (Baisas and Ubaldo Pagayon, 1952; Belkin, 1955), *Orthopodomyia* (*O. alba* Baker and *signifera* Coqt.; Carpenter and La Casse, 1955) and *Culicoides* (*C. nubeculosus* Meig.; Kettle and Lawson, 1952).

In other cases the differences of the early stages to which differences of the adult do not correspond may indicate biological or ecological races, e.g., in *Hemipenthes morio* L., where two different pupal forms have been obtained from the different hosts *Banchus* and *Ernestia* (Gäbler, 1949), or in Simuliidae where the striking pupal forms have been interpreted variously as species or simple modifications (Tonnoir, 1925; Freeman and de Meillon, 1953). In the blepharocerid *Bibiocephala*, larval and pupal forms not reflected in the adults have been found both in the United States (Johannsen, 1934) and in Japan (Kitakami, 1931). Among lower insects the Callaphididae contain species that are not separable as alates but are clearly distinct as young larvae (Quednau, 1954).

Where the special forms of the early stages are so conspicuously different as in *Meloë violaceus*, *Orthopodomyia*, and *Trachys griseofasciata*, and where they occur in the same area, as is the case in these forms, they must necessarily be regarded as good species. As all inheritance of characters proceeds only by way of the adult there is of course no question of separate "larval or pupal species" in the true sense of the word. Where such terms are used, they are applied in a loose sense. However different egg, larva, pupa, and adult may be from one another they combine to form the species, and a sufficiently careful examination will be expected sooner or later to reveal specific differences in those stages in which the species are so far indistinguishable. Thus, the significance of "larval or pupal species" is not one of principle but rather one of degree. These species and the more numerous ones in which, in addition to certain early stages, at least one sex of the adult is separable, though the former more readily (Emden, 1957), only show that the amplitude of interspecific variation is not necessarily greatest in the adult. Undoubtedly many more cases in which the early stages are more clearly distinguished than the adults will be discovered as the knowledge of the larvae etc. becomes more complete and as the appreciation of larval characters improves. It is perhaps too early yet to prophesy whether the early stages are likely to prove quite as suitable for the distinction of species as the adults. However, as far as the latter are more highly differentiated, which is normally the case, there is much reason to think that the view will be confirmed that in most cases species and infra-specific groups will remain more clearly indicated in the adult than in the early stages, in spite of cases like *Meloë violaceus* in which the larvae differ so much more strikingly than the adult.

REFERENCES

Baisas, F. E., and A. Ubaldo-Pagayon, 1952. Notes on Philippine mosquitoes XVI, genus *Tripteroides*. *Mon. Inst. Sci. Technol. Manila* 2: 1–198.

Belkin, J. N. 1955. The *Tripteroides caledonica* complex of mosquitoes in Melanesia. *Pacific Sci.* 9: 221–246.

Blair, K. G. 1942. The first-stage larva of *Meloë violaceus* Marsh. *Ent. Mon. Mag.* 78: 112–116.

Carpenter, S. J., and W. J. LaCasse. 1955. Mosquitoes of North America. *University of California Press*, Berkeley, Calif. 360 pp.

Cros, A. 1929. Notes sur les larves primaires des Meloidae. *Ann. Soc. ent. France* 98: 193–222.

Cros, A. 1934. Sur le *Pediculus melittae* Kirby. *Ann. Sci. Nat., Zool.* (10) 17: 59–66.

Emden, F. I. van. 1943. Larvae of British beetles IV, various small families. *Ent. Mon. Mag.* 79: 209–223, 259–270.

Emden, F. I. van. 1957. The taxonomic significance of the characters of immature insects. *Annual Rev. Ent.* 2: 91–106.

Freeman, P., and B. de Meillon. 1953. Simuliidae of the Ethiopian Region. British Museum (Nat. Hist.), London. 224 pp.

Gäbler, H. 1949. Beitrag zur Kenntnis der forstlich wichtigen Trauerschweber. *Nachrbl. deut. Pflschutzd.* (N.F.) 3: 55–57.

Johannsen, O. A. 1934. Aquatic Diptera I. Nematocera exclusive of Chironomidae and Ceratopogonidae. *Cornell Univ. Agr. Exp. Sta. Mem.* 164: 1–71.

Kettle, D. S., and J. W. H. Lawson. 1952. The early stages of British biting midges Culicoides, etc. *Bull. ent. Res.* 43: 421–467.

Kitakami, S. 1931. The Blepharoceridae of Japan. *Mem. Coll. Sci. Kyoto Imp. Univ.* (B) 6: 52–108.

Newport, G. 1851. On the natural history, anatomy and development of the oil beetle *Meloë* etc. *Trans. Linn. Soc. Lond.* 20: 297–320, 321–357.

Quednau, W. 1954. Monographie der mitteleuropäischen Callaphididae I. Die Junglarven des ersten Stadiums der mitteleuropäischen Callaphididae. *Mitt. Biol. Zentralanst. Forst- u. Landw. Berlin- Dahlem* 78: 1–71.

Singh, B. 1953. Immature stages of Indian Lepidoptera 8. Geometridae. *Indian For. Rec.* (*N. S.*), *Ent.* 8: 63–158.

Tonnoir, A. L. 1925. Australasian Simuliidae. *Bull. ent. Res.* 15: 213–255.

Yano, T. 1952. The developmental stages of two genera of Trachyinae, *Trachys* and *Habroloma*, of Shikoku, Japan. *Trans. Shikoku Ent. Soc.* 3: 17–40.

DISCUSSION

J. OBENBERGER. There are two different larval forms, in *Tilia* and in *Salix*, and only one imaginal form in *Trachys minuta* (F.).

F. I. VAN EMDEN. The case of *Trachys minuta* seems to be strictly comparable to that of *T. griseofasciata*, and I am glad to have it brought to my attention.

Etudes systématiques et zoogéographiques sur les Cynipidés (Hyménoptères)

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RÉSUMÉ

La présente communication est un conspectus de tous les genres et de toutes les espèces de notre pays qui ont été décrites jusqu'à présent. On indique ainsi que 3 familles avec 5 sous-familles comprenant un nombre total de 37 genres et 120 espèces sont représentées dans la faune de la République Populaire Roumaine. Tous ces genres et toutes ces espèces sont rassemblés dans un tableau synoptique qui indique aussi leur répartition en Europe.

En Roumanie, de tous les groupes de Cynipidés, les Cynipinae sont les mieux étudiés. Des 70 genres de Cynipinae décrits sur le globe entier, on connaît en Roumanie 25 genres, dont 21 genres, comprenant 94 espèces, produisent la gale, tandis que 4 genres comprenant 12 espèces sont commensaux. Il y a, en tout, 106 espèces de Cynipinae.

En ce qui concerne les relations zoogéographiques entre la faune des cynips de Roumanie et celle d'Europe, on constate que parmi les 120 espèces citées jusqu à présent dans la République Populaire Roumaine, un nombre de 110 espèces se trouvent aussi dans la faune de l'Europe centrale, 6 espèces proviennent du sud de l'Europe (d'Europe méridionale), une espèce est originaire du Sud-Est de l'Europe (Adleria gallae-tinctoria *(Ol.)*), *tandis qu'une espèce provient de la partie méridionale de la Russie européenne* (Panteliella fedtschenkoi *Rubsaamen). Deux formes sont endémiques pour la faune de notre pays* (Rhynchacis istratii *Kieffer, 1900, et* Diglyphosema jacqueti *Kieffer, 1900).*

Les premières études de zoologie, dans notre pays, datent du dix-huitième siècle, concernant surtout les animaux vertébrés. L'entomologie commença à préoccuper les zoologues roumains vers la moitié du dix-neuvième siècle et, parmi les premiers groupes d'insectes étudiés, on compte aussi les Hyménoptères.

En ce qui concerne les Cynipidés, les premières observations ont été faites après 1900, au cours d'études cécidologiques générales qui n'intéressaient que le point de vue botanique puisqu'elles se limitaient à décrire les espèces de galles mais non les insectes respectifs (Borcea, 1914; Brandza, 1914–1916). Par la suite, d'autres travaux de cécidologie ont encore été faits mais toujours sans l'étude entomologique des zoocécidés respectifs (Borza et Ghiuta, 1938–46; Geburtig, 1932; Ghiuta, 1937–1945), n'enrichissant que les connaissances de cécidologie.

Cette lacune, qui existait dans l'étude des Cynipoïdés de notre pays, est actuellement comblée par les recherches qui s'encadrent dans une grande étude faunistique éditée par l'Académie de la République Populaire Roumaine et intitulée "La faune en R.P.R.". La série des monographies sur la faune en R.P.R. apparues depuis 1949 jusqu'à ce jour, comprend également les travaux d'entomologie suivants: Protura, Diplura, Isoptera, Thysanoptera, Cicindellidae, Carabidae, Melonthinae, Rutelinae, Bombinae. Comme toutes les autres monographies sur la faune de R.P.R., ces travaux contiennent tout ce que l'on connaît sur ces groupes respectifs dans notre pays, tant au point de vue systématique que zoogéographique. Actuellement, dans ce même cadre, d'autres groupes d'insectes sont étudiés et parmi eux se trouvent les Cynipoïdés pour lesquels un matériel important a été accumulé permettant des considérations systématiques et zoogégraphiques sur cette importante superfamille d'insectes.

Les études sur les Cynipoidés sont importantes pour notre pays tant au point de vue systématique et zoogéographique pour la connaissance des formes qui vivent ici et leurs aires géographiques, qu'au point de vue pratique.

Le côté pratique de ces recherches résulte de ce que la grande majorité des espèces de Cynipidés de notre pays produisant des galles surtout sur les espèces de *Quercus*, arbres qui ont une grande importance dans notre pays, formant de vastes forêts dans les régions de plaine jusqu'à l'altitude de 400 mètres. Dans l'Europe entière on connaît environ 177 espèces de Cynipidés gallicoles sur les arbres et les arbustes des forêts. Parmi elles, 95 espèces ont été décrites en République Populaire Roumaine. Dans l'est de l'Europe, le nombre de ces espèces est moindre, c’est ainsi qu’en U.R.S.S. on ne connaît que 39 espèces de cette catégorie.

Sans donner trop d’exemples sur le mode d’endommagement causé aux arbres de notre pays par les cynips nous montrerons cependant que l’action de certaines espèces sur les plantes a souvent comme résultat une croissance désordonnée de la plante attaquée qui est surtout provoquée par la destruction des bourgeons terminaux. C’est en spécial sur les jeunes arbres que cette action est surtout redoutable. Si les arbres ne sont pas, à proprement dit, détruits puisqu’ils ne se dessèchent pas et ne meurent pas, pourtant ils ne se développent plus normalement, leur croissance devient irrégulière, très ralentie et les plantes prennent un aspect buissonneux. Ce sont des effets de ce genre que produisent habituellement *Adleria conglomerata*, *Adleria kollari*, *Synophrus politus*, *Biorhiza pallida*, *Andricus multiplicatus*, etc. Certaines galles d’entre celles qui se développent sur les feuilles sont parfois en si grand nombre qu’elles recouvrent toute la surface de la feuille, diminuant beaucoup de cette façon le pouvoir végétatif de la plante. L’attaque de ces insectes a lieu aussi surtout sur les jeunes arbres et sur les arbres des clairières, c’est-à-dire justement sur les arbres plantés pour recouvrir une certaine surface, un vide, ou pour créer un rideau forestier de protection. C’est de cette manière que se produit l’attaque de *Cynips pubescens*, *Cynips quercus folii*, *Neuroterus baccarum*, etc.

Mais même les vieux arbres subissent souvent de grands dommages à cause des Cynipidés. Pour ces arbres le problème de leur bon développement ne se pose plus, en revanche à la suite de l’attaque des Cynipidés, la production des fruits (glands) diminue souvent jusqu’à sous 50 pour-cent. Parmi les espèces qui endommagent le gland, dans notre pays, les plus importantes et les plus répandues sont *Adleria quercus calicis* et *Adleria caput medusae.*

La faune des Cynipidés en R. P. R. est représentée par trois des quatre familles qui existent sur tout le globe (d’après la classification de L. H. Weld de 1952). Ces familles sont: Ibaliidae, avec un genre et une espèce; (Aspicerinae, Anacharitinae, Figitinae), comprenant un nombre de 5 genres et 6 espèces; Cynipidae (Eucoilinae et Cynipinae), avec un nombre de 30 genres et 113 espèces.

Par rapport aux quatre familles avec 10 sous-familles et 177 genres qui sont connus sur tout le globe, dans la faune de R. P. R. sont représentés 3 familles avec 5 sous-familles et un nombre total de 36 genres et 120 espèces.

Dans notre pays, ce sont les Cynipinés qui, de tous ces groupes de Cynipoïdés sont le mieux étudiés. Des 70 genres de Cynipinés décrits sur le globe entier, en Roumanie on connaît 24 genres, parmi lesquels 20 sont gallicoles comprenant 95 espèces et 4 avec 12 espèces sont des Cynipinés commensaux soit au total 107 espèces de Cynipinés.

Les genres de Cynipinés représentés dans la faune de R. P. R. sont les suivants: *Neuroterus* avec 10 espèces, *Cynips* avec 5 espèces, *Trigonaspis* avec 2 espèces, *Biorhiza* avec une espèce, *Chilaspis* avec une espèce, *Aphelonyx* avec une espèce, *Adleria* avec 21 espèces, *Andricus* avec 31 espèces, *Synophrus* avec une espèce, *Saphonecrus* avec une espèce, *Synergus* avec 8 espèces, *Ceroptres* avec une espèce, *Periclistus* avec 2 espèces, *Xestophanes* avec une espèce, *Diastrophus* avec 2 espèces, *Aylax* avec 3 espèces, *Liposthenes* avec une espèce, *Isocolus* avec une espèce, *Aulacidea* avec 2 espèces, *Penteliella* avec une espèce, *Diplolepis* avec 6 espèces, *Pediaspis* avec une espèce, *Calirrhytis* avec une espèce. (Nomenclature d’après L. H. Weld, 1952).

De cette énumération, on observe qu’au nombre relativement grand, de 24 genres (par rapport aux 70 connus sur tout le globe), ne correspondent dans notre pays qu’un petit nombre d’espèces, au total 120. On remarque, en effet, que seulement deux genres ont plus de 10 espèces, soit *Andricus* avec 31 espèces et *Adleria* avec 21 espèces; un genre a 10 espèces, c’est *Neuroterus;* les autres genres ont moins de 10 espèces et parmi eux 12 genres n’ont qu’une seule espèce.

En ce qui concerne les Cynipoïdés parasites, des recherches qui ont été effectuées jusqu’à présent dans notre pays, il résulte que pour les 11 genres connus correspondent 13 espèces. Ces formes sont les suivantes: *Cothonaspis* avec une espèce, *Eucoila* avec une espèce, *Lytosema* avec une espèce, *Rhyncacis* avec une espèce, *Microstilba* avec une espèce, *Digliphosema* avec deux espèces, *Aspicera* avec une espèce, *Anacharis* avec une espèce, *Sarothrus* avec une espèce, *Amblynotus* avec une espèce, *Figites* avec deux espèces. On observe que 9 de ces genres n’ont qu’une seule espèce décrite dans notre pays.

LES CYNIPOIDES DE ROUMANIE	Toute l'Europe	Europe centr. et merid.	Europe centr. et occid.	Europe centrale	Europe merid.	Europe merid. et orientale	Europe orientale	Communes	Rares	♂♂
Adleria conifica Htg.		+	+					+		
amblicera Gir.		+						+		
kollari Htg.		+	+					+		
lignicola Htg.		+	+					+		
gallae-tinctoriae (01.)						+		+		
caliciformis Gir.		+						+		
ambigua Trotter					+				+	
corruptrix Schltd.		+							+	
galleata Gir.		+						+		
conglomerata Gir.		+	+					+		
polycera polycera Gir.		+						+		
tomentosa Trotter					+				+	
mitrata Mayr		+							+	
coriaria coriaria Htg.		+						+		
coronata Gir.		+						+		
hungarica Htg.				+				+		
quercus tozae Bosc.		+						+		
truncicola Giraud		+						+		
caput medusae Gir.		+						+		
quercus calicis Burg.		+	+					+		
Adleria *hartigi* Hartig		+							+	
Andricus *cicrulans* Mayr			+						+	+
testaceipes testaceipes Htg.	+								+	+
quercus radicis q. *radicis* (F.)	+							+		+
quercus corticis (L.)	+								+	
fecundatrix (Htg.)	+							+		
ostrea (Htg.)	+							+		
inflator Htg.	+							+		+
curvator curvator Htg.	+							+		+
callidoma Htg.		+	+					+		+
quercus ramuli q. *ramuli* (L)	+								+	+
marginalis Schltd.			+					+		

LES CYNIPOIDES DE ROUMANIE	Toute l'Europe	Europe centr. et merid.	Europe centr. et occident.	Europe Centrale	Europe merid	Europe merid. et orientale	Europe Orientale	Communes	Rares	♂♂
seminationis Giraud			+						+	
rhyzomae (Htg.)					+				+	
superfetationis (Gir.)		+						+		
solitarius (Fonsc.)	+							+		
giraudianus D.T. et Kieffer		+							+	
histrix Trotter					+			+		
seckendorffi (Wachtl)		+							+	
panteli panteli Kieffer					+				+	
mayri Wachtl		+							+	
Andricus lucidus lucidus (Htg.)		+	+					+		
gemmea (Gir.)		+						+		
sufflator Mayr					+			+	+	
crispator Tschek		+							+	+
crispator Tschek		+							+	+
adleri Mayr			+						+	+
cydoniae Giraud		+							+	+
multiplicatus Giraud		+						+		+
aestivalis Giraud		+							+	+
grossulariae Giraud		+							+	+
vindobonensis Müllner				+					+	+
albopunctatus (Schltd.)	+								+	
Synophrus politus Htg.		+						+		+
Saphonecrus undulatus (Mayr)				+				+		+
Synergus reinhardi Mayr		+	+						+	+
hayneanus (Ratz.)		+						+		+
variabilis Mayr		+						+		+
nervosus Htg.			+						+	+
pallicornis Htg.		+	+					+		+
tscheki Mayr		+	+						+	+
Synergus albipes Htg.			+						+	+
thaumacerus (Dalm.)	+								+	+
Ceroptres arator Hartig	+							+		+

LES CYNIPOIDES DE ROUMANIE	Toute l'Europe	Europe centr. et merid.	Europe centr. et occident.	Europe Centrale	Europe merid.	Europe merid. et orientale	Europe orientale	Communes	Rares	♂ ♂
Periclistus brandti (Ratz.)	+								+	+
caninae (Htg.)			+						+	+
Xestophanes potentillae (Ratz.)	+								+	+
Diastrphus rubi (Bouché)	+							+		+
mayri Reinh.			+					+		+
Aylax kerneri (Wachtl)		+						+		+
salviae (Gir.)		+							+	+
papaveris (Perris)	+								+	+
jaceae (Schenck)			+					+		+
Liposthenes glechomae (L.)				+				+		
Isocolus scabiosae Giraud	+								+	
Aulacidea pilosellae (Kieffer)			+					+		
hieracii (L.)	+							+		+
Panteliella fedtschenkoi Rübs					+	+		+		
Timaspis phoenixopodos Mayr			+						+	+
lampsanae (Perris)			+	+					+	
Diplolepis eglanteriae Htg.	+							+		+
rosarum Giraud		+	+					+		
Diplolepis spinosissimae Giraud		+	+					+		+
centifoliae Htg.				+					+	+
mayri Schltd.		+	+						+	
rosae (L.)	+							+		
Pediaspis aceris (Gm.)			+						+	+
Callirhytis glandium (Gir.)		+	+						+	
Ibalia leucospoides Hochenw.	+								+	+
Cothonaspis (Ch.) *rapae* (Westw.)			+						+	+
Eucoila fungicola Kieffer			+						+	+
Lytosema guerini (Dahlb.)		+	+						+	+
Rhynchacis istratii Kieffer						+			+	+
Microstilba heterogena Gir.				+					+	+
Diglyphosema jacqueti Kieffer						+			+	+
Aspicera scutellata Villers	+								+	+

LES CYNIPOIDES DE ROUMANIE	Toute l'Europe	Europe centr. et merid.	Europe centr. et occident.	Europe centrale	Europe merid.	Europe merid. et orientale	Europe orientale	Communes	Rares	♂ ♂
Anacharis tipica Wlk.			+						+	+
Sarothrus tibialis (Zett.)			+						+	+
Amblynotus opacus (Htg.)	+								+	+
Figites scutellaris scutellaris Rossi	+								+	+
consobrinus Giraud			+						+	+
Neuroterus aprilinus (Giraud)		+	+					+		+
lanuginosus (Giraud)		+						+		
minutulus Giraud		+							+	
saliens (Kollar)		+						+		
glandiformis (Giraud)		+							+	+
fumipennis (Htg.)	+							+		+
laeviusculus (Sch.)	+							+		
baccarum (L.)	+							+		+
numismalis (Fourc.)		+	+					+		+
macropterus (Htg.)		+						+		
Cynips quercus folii L.	+							+		+
longiventris (Htg.)		+						+		+
divisa (Htg.)		+	+					+		
querus Fourc.		+						+		
agama (Htg.)		+	+					+		
Trigonaspis megaptera Panz.	+							+		+
synaspis (Htg.)	+							+		
Biorhiza pallida (Olivier)	+							+		+
Chilaspis nitida (Gir.)				+				+		+
Aphelonyx cerricola (Gir.)		+						+		

L'observation générale sur la composition faunistique des Cynipoïdés de Roumanie conduit à la conclusion que cette faune est riche en genres et pauvre en espèces. Les recherches actuelles, et celles qui seront effectuées à l'avenir, vont enrichir l'inventaire des formes connues mais il ne semble pas que la proportion d'entre le nombre de genres et le nombre d'espèces soit modifiée.

Par sa position géographique, la République Populaire Roumaine, située au Sud-Est de l'Europe à l'embouchure du Danube dans la Mer Noire, se trouve à un tripe croisement au point de vue de la distribution géographique de la faune et de la flore. Notre pays se rattache à la faune de l'Europe centrale et occidentale, à la faune de l'Europe du Sud et à celle de l'Europe orientale, de la partie européenne de l'union Soviétique.

Elle se rattache à la faune de l'Europe centrale par sa faune de forêt; par la faune de steppe, de terrains ouverts, elle se rattache à la faune des steppes pontiques de l'ouest de notre pays; par la faune de Dobroudja et du sud du pays, notre faune se rattache à la faune de la péninsule balkanique et de l'Asie Mineure; par la faune du Banat et du nord de l'Olténie, elle se rattache à la région occidentale de la Péninsule balkanique ainsi qu'à la faune méditerranéenne de l'Italie et des autres régions du Sud de l'Europe.

Pour illustrer d'une manière plus concrète les liaisons zoogéographiques de la faune des Cynipoïdés de Roumanie avec la faune des Cynipoïdés de l'Europe, nous présentons le tableau suivant, qui comprend toutes les espèces de Cynipoïdés connues en R.P.R. et leur distribution en Europe.

De ce tableau formé de toutes les 120 espèces de Cynipoïdés (95 espèces gallicoles, 12 espèces commensales, et 13 espèces parasites), on observe que:

Trente espèces sont des formes qui sont répandues dans toute l'Europe. Parmi elles, citons: *Neuroterus fumipennis* (Htg.), *Neuroterus baccarum* (L.), *Trigonaspis megaptera* Panz., *Andricus fecundatrix* (Htg.), *Andricus inflator* (Htg.), *Ceroptres arator* (Htg.), *Diastrophus rubi* Bouché.

Cinquante-six espèces se trouvent dans la faune de l'Europe centrale et méridionale et parmi elles, on trouve les formes suivantes: *Neuroterus lanuginosus* (Gir.), *Neuroterus numismalis* (Fourc.), *Cynips longiventris* (Htg.), *Cynips agama* (Htg.), *Aphelonyx cerricola* (Gir.), *Adleria caliciformis* (Gir.), *Adleria coronata* (Gir.), *Adleria caput medusae* (Htg.), *Synergus variabilis* (Mayr), *Aylax Kerneri* (Wachtl).

Trente-neuf espèces se trouvent dans la faune de l'Europe centrale et occidentale et parmi elles les formes *Andricus adleri* (Mayr), *Andricus circulans* (Mayr), *Andricus marginalis* (Schltd.), *Aylax jaceae* (A. Schenck), *Synergus nervosus* (Htg.), *Eucoila fungicola* (Wlk.).

Six espèces se trouvent uniquement dans la faune de l'Europe centrale et parmi elles: *Chilaspis nitida* (Gir.), *Adleria hungarica* (Htg.), *Saphonecrus undulatus* (Mayr), *Diplolepis centifoliae* (Htg.).

Six espèces appartiennent à la faune de l'Europe méridionale, dont: *Andricus histrix* Trotter, *Andricus panteli panteli* Kieffer, *Adleria tomentosa* Trotter.

Une espèce est une forme sud-est européenne: *Adleria gallaetinctoriae* Olivier.

Une espèce est originaire de l'Est (sud de la partie européenne de l'Union Soviétique): *Panteliella fedschenkoi* Rübsaamen.

Dans la faune des Cynipoïdés de R.P.R., se trouvent également deux formes endémiques, les seules qui soient décrites jusqu'à ce jour: *Rhynchacis istrattii* Kieffer, 1900, et *Diglyphosema jacqueti* Kieffer, 1900.

De l'analyse de l'ensemble de ces données systématiques et zoogéographiques, il résulte que du nombre total de 120 espèces de Cynipoïdés connues dans la faune de R.P.R., 110 espèces vivent également dans l'Europe centrale. Le caractère zoogéographique des Cynipoïdés de R.P.R. est donc de toute évidence central européen. Ceci concorde d'ailleurs tant avec l'extension des provinces biogéographiques de la Roumanie, provinces parmi lesquelles justement celle qui a des liaisons directes avec l'Europe centrale (province dacique), est la plus étendue, qu'avec le caractère général de la faune de Roumanie qui est central européen.

BIBLIOGRAPHIE

Baudiš, E. 1939. Contribution à l'extension des zoocécidies de la Roumanie. *Bul. grad. bot. Cluj.* 19.

Baudiš, E. 1946. Fourth contribution to the knowledge of plant galls in Bohemia. *Acta entomologica musei nationalis pragae* 24.

Baudiš, E. 1947. Sixth contribution to the zoocecidiological research of Moravia and Silesia. *Acta universitatis agriculturae et silviculturae.* Brno.

Baudiš, E. 1948. The seventh contribution to the zoocecidiological investigation of Moravia and Silesia. *Acta universitatis agriculturae et silviculturae.* Brno.

Belizin, V. I. 1951. Orehotvorchi (Hymenoptera: Cynipidae) faunî S.S.S. R. i sopredelnîh stran. *Entomologicescoe obozrenie* 31.

Borcea, I. 1914. Zoocécidies de Roumanie. *Ann. sc. Univ. Jassy* 7.

Borza, A., et M. Ghiuta, 1938–46. Contributii la studiul și răspîndirea cecidiilor în Romînia. *Bul. grad. botanice Cluj.* 18–26.

Brandza, M., 1914–1916. Contribution à l'étude des zoocécidies de Roumanie. *Ann. sc. Univ. Jassy* 8–10.

Dalla-Torre, K. W., und J. J. Kieffer. 1910. Cynipidae. Das Tierreich. Lief. 24. Berlin.

Geburtig, T. 1932. Nouvelles galles pour Roumanie. *Publ. Soc. Nat. Rom.*, Nr. 10.

Ghiuta, M. 1937–1945. Contributii la studiul și răspîndirea cecidiilor in Romînia. *Bul. grad. bot. Cluj.* 17–25.
Henrich, C. 1916. Pflanzengallen (Cecidien) der Umbebung von Hermannrstadt. *Verh. u. Mitt. d. Sieb. ver. f. Nat. zu Hermennstadt.* 66.
Ionescu, M. 1955. Contributii la studiul Cynipidelor din R.P.R. *Revista Universitatii C. I. Parhon.*
Ionescu, M. 1956. Noi contributii la studiul Cynipidelor din R.P.R. *Bul. st. Acad. R. P. R.*
Ionescu, M., si N. Roman. 1956. Contributiuni la studiul Zoocecidiilor din R. P. R. *Revista Universitatii C. I. Parhon.*
Rübsaamen, E. 1895–1896. Ueber russiche zoocecidien. *Bul. Soc. Imp. Nat. Moscou.*
Rübsaamen, E. 1900. Ueber Zoocecid. d. Balkan-Halbinsel. *Illustr. Zeitschr. f. Ent.* 5.
Sevcenco, M. I. 1952. C. voprosu o geograficencom rasprostranenii cesohoziaistvennom znacenii dubovîh orehotuorc (Cynipidae) C. C. C. R. *Zoologiceschii jurnal.* 31.
Weld, L. H. 1952. Cynipoidea 1905–1950. Privately printed. Ann Arbor, Michigan.

Morphological Variations in Populations of the Larch Sawfly, *Pristiphora erichsonii* (Htg.) (Hymenoptera: Tenthredinidae), from Canada, Great Britain, and Japan[1]

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ABSTRACT

A morphological comparison was made of adult females of the larch sawfly, Pristiphora erichsonii *(Htg.) from Great Britain, Canada, and Japan. Four characters, three measurable and one descriptive, were employed. Morphometric analyses of these characters showed that the populations from the three countries were separable and that there was a closer affinity between Canadian and Japanese populations than between Canadian and British populations.*

INTRODUCTION

The larch sawfly, *Pristiphora erichsonii* (Htg.), is circumpolar in distribution and is currently a pest of economic importance in Canada. The resurgence of the sawfly population in Central Canada was associated with the development of an immunity reaction to the introduced parasite *Mesoleius tenthredinis* Morley (Muldrew, 1955). The question arose if the resistant and the susceptible populations of sawflies were morphologically and biologically similar. Sawfly resistance to *M. tenthredinis* had not been recorded in Great Britain at that time; therefore a comparative study of this species from both Great Britain and Canada was begun. It was also hoped that evidence sufficient to clarify the taxonomic status and origin of the larch sawfly in Canada would be obtained.

The discovery of encapsulation in England by M. G. Maw (pers. comm.), in 1955, precluded any attempt to correlate morphological differences to susceptibility or resistance to *M. tenthredinis*. The morphological study, however, indicated apparent differences, and the data herein presented are the results of the first phase of the investigation: the comparison of sample populations of *P. erichsonii* adults from Great Britain and Canada. Adult specimens of Japanese origin were also studied.

MATERIAL AND METHODS

Pinned and preserved adults of *P. erichsonii* were obtained from collaborators in Great Britain, Japan, and Canada. These were supplemented with adults reared at the Belleville laboratory from field collections of both larvae and cocoons made in Great Britain and Canada.

Adults were killed 24 hours after emergence to ensure complete pigmentation and wing expansion. Approximately 3,000 slides of the wings, antennae, lancets, and ovipositor sheaths were made, as well as over 350 mounts of the heads of the adults.

Extreme care was taken in the final selection of characters for the study. Nine characters in all were employed; however, five of these (width and length of ocellar triangle, width and length of head capsule, colour and colour pattern, ovipositor sheath, and lancet) proved useless. The four remaining have been used for species separation by many authors and are as follows: length and width of pentagonal area (Enslin, 1918); lengths of third and fourth antennal segments (Cresson, 1880, Cameron, 1885, Packard, 1890, Marlatt, 1896, Hewitt, 1912, MacGillivray, 1917, and Dobrodeiev, 1921); length of antenna and costa plus stigma (Benson, 1952); and structure of the median fovea (Cameron, 1885, Marlatt, 1896, Hewitt, 1912, MacGillivray, 1917, and Enslin, 1918). These characters are shown in Figs. 1–4.

All measurements were made and checked with a compound microscope fitted with an ocular micrometer. The measurements were tabulated and the data analysed statistically.

USE OF THE PENTAGONAL AREA INDEX

The width (X1) and the length (X2) of the pentagonal area (Fig. 2) was measured for 221 adult females of *P. erichsonii* from Canada, 58 from Great Britain, and 22 from Japan.

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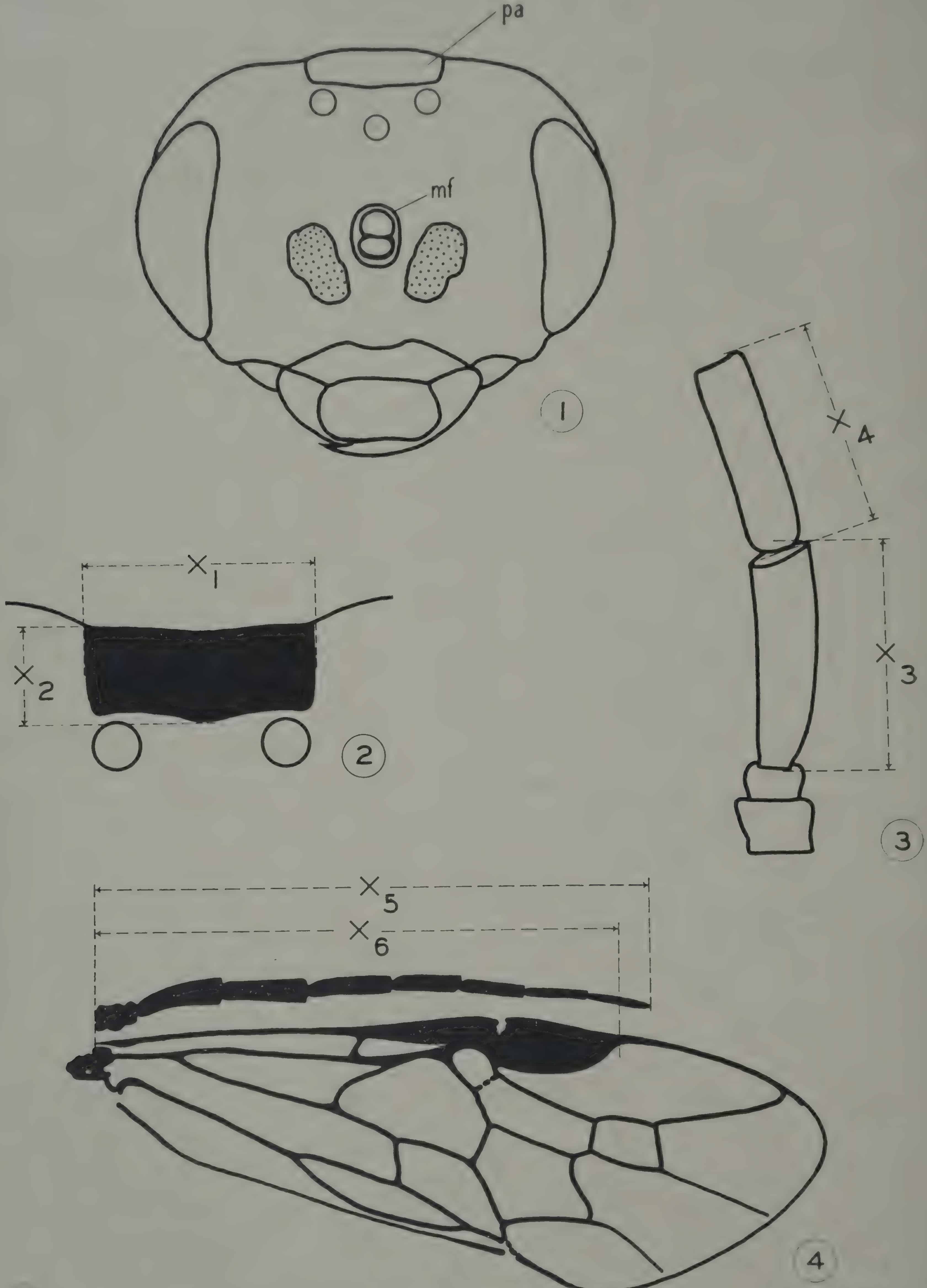


Fig. 1. Anterior aspect of head of *P. erichsonii* showing relative position of median fovea (*mf*) and pentagonal area (*pa*). Fig. 2. Pentagonal area. Fig. 3. Antennal segments three and four. Fig. 4. Lengths of antenna and costa plus stigma.

These measurements were used in the form of an index (X1 X2), because of the overall size differences within and between series, as a means of separating the adults from the three countries.

To determine the efficiency of this index, the hypothesis was made that the samples were drawn from the same population. The calculation in the form of an analysis of variance

(Table I) indicated that the difference of the samples between countries was highly significant ($P < .01$).

TABLE I. Analysis of Variance of Pentagonal Area (X1/X2) of 301 Specimens in Three Countries.

Source	d.f.	S.S.	M.S.	F.
Samples	300	20.880		
Country Means	2	19.122	9.561	1593.5*
Error	298	1.758	0.006	

*Significant at 1% level.

Further analysis by the application of a t-test (Table II) to the same population data showed that the differences between any two countries, e.g. Canada vs. Great Britain, Canada vs. Japan, and Great Britain vs. Japan, were also highly significant ($P < .001$).

TABLE II. T-test and Coefficient of Difference for Pentagonal Area (X1/X2) Between Countries.

Country	t	Coefficient of Difference	Nonoverlap Per Cent	d.f.
Canada vs. Great Britain	44.5*	2.976	100	277
Canada vs. Japan	26.9*	2.844	100	241
Great Britain vs. Japan	36.3*	6.556	100	78

*Significant at .1% level.

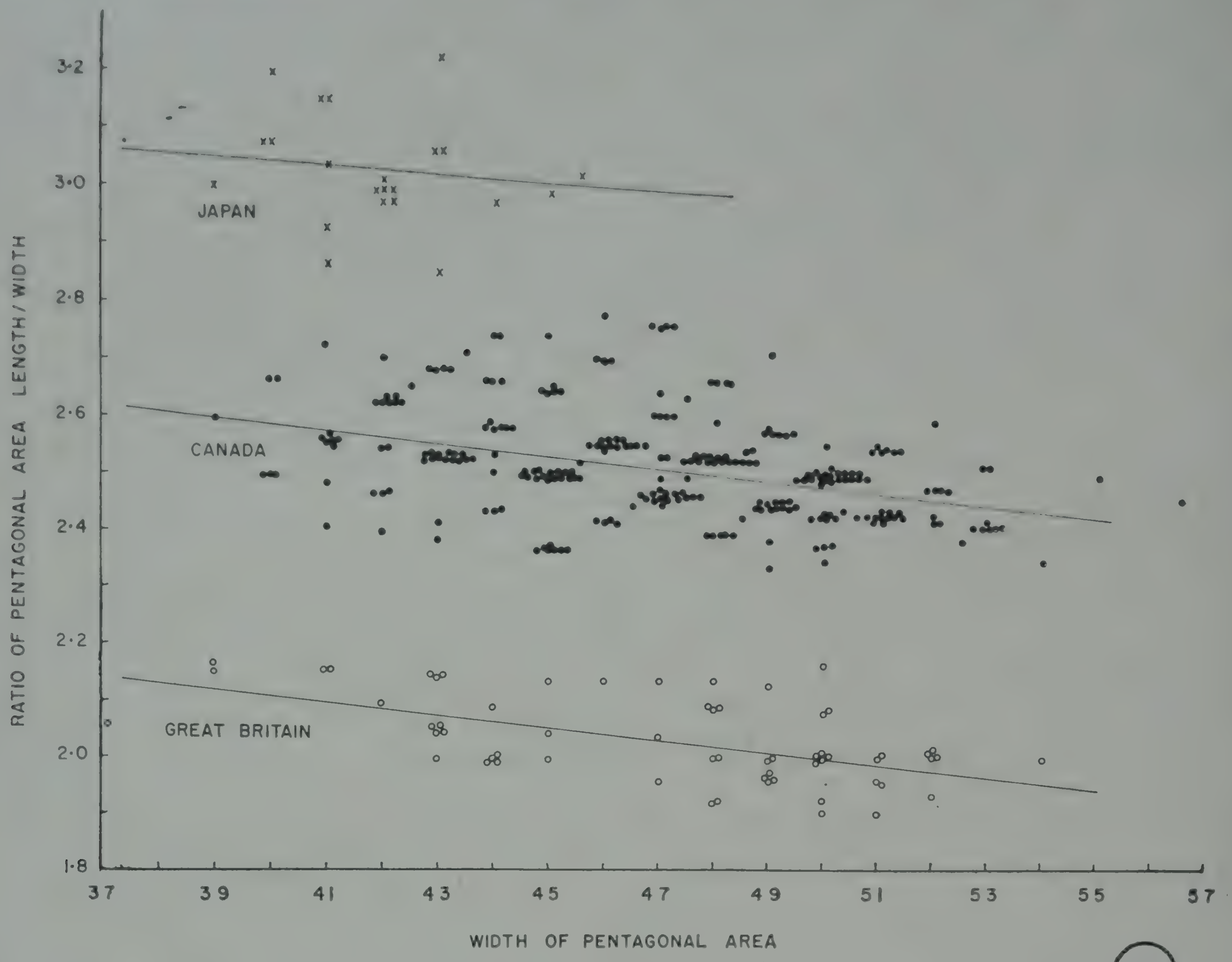
Though the difference with both the analysis of variance and the t-test was highly significant, a check of the percentage nonoverlap between countries was made to confirm the results. A variation of the conventional "75 per cent rule", used by some taxonomists for determining subspecific distinctness and called the coefficient of difference by Mayr, Linsley, and Usinger (1953), was applied. This coefficient was of such a magnitude that 100 per cent nonoverlap occurred between the three countries (Table II).

Quantitative data for this particular character lend themselves readily to visual presentation. The sample populations are separate entities and their ratio means are approximately 2.00 for Great Britain, 2.50 for Canada, and 3.00 for Japan. The scatter diagram (Fig. 5) clearly shows the allometric relationship of the length and width characters for the three populations.

The correlation coefficients were calculated by using the pentagonal area index (X1/X2) against the width (X1). In all instances the coefficients were negative, significantly so for Canada and Great Britain ($P. < .01$) and showing a strong relationship, but not significant for Japan ($P > .05$) and showing a weaker relationship or less deviation from linearity. This indicates the usefulness of the regression line and the relationship of the quantitative characters to one another. Regression lines (Fig. 5) superimposed on the scatter diagram showed that, for all populations, an increase in the width of the pentagonal area is associated with a decrease in its ratio.

USE OF THE ANTENNAL SEGMENT INDEX

The lengths of the third (X3) and fourth (X4) antennal segments (Fig. 3) were measured from 431 antennae of specimens from Canada, 114 from Great Britain, and 42 from Japan. These measurements were used in the form of an index (X3/X4), as with the pentagonal area.



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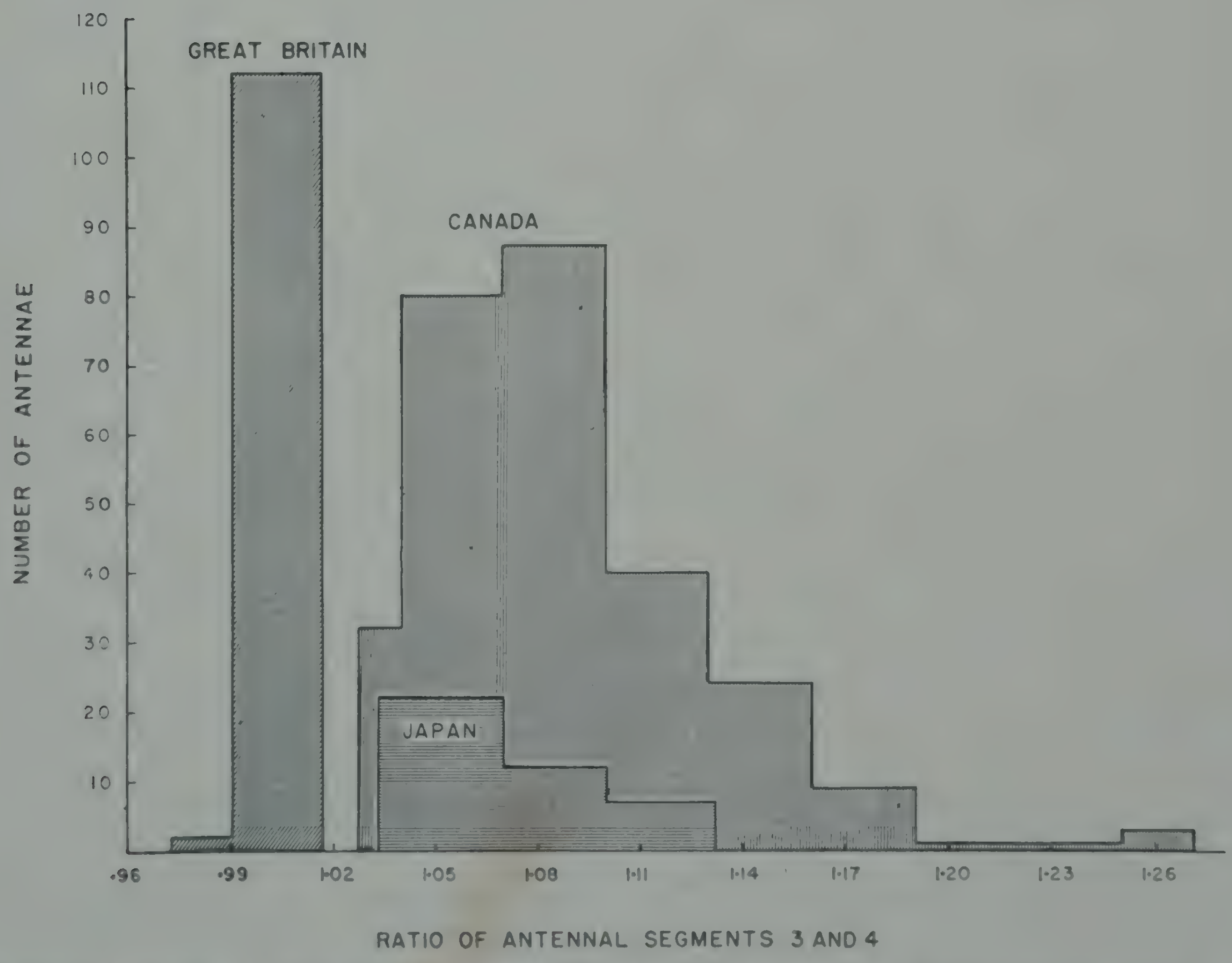

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Fig. 5. Scatter diagram of pentagonal area index and regression lines for sample populations of *P. erichsonii* from Great Britain, Canada, and Japan. Fig. 6. Histogram of antennal segment index from sample populations of *P. erichsonii* from Great Britain, Canada, and Japan.

The same hypothesis was suggested with this character as with the pentagonal area index and the same statistics employed. The analysis of variance (Table III) showed a significant difference for this character in the sample populations from the three countries

(P<.01). The t-test (Table IV) also showed the differences between any two countries to be highly significant (P<.001). The difference between Canada and Japan, though highly significant, was smaller than the differences between any two other countries. The true significance of this difference was clearly illustrated by the application of the coefficient of difference (Table IV). The percentage nonoverlap between Canada and Great Britain and Great Britain and Japan was 100, but the percentage nonoverlap between Canada and Japan was less than 75.

TABLE III. Analysis of Variance of Antennal Segments Three and Four (X3/X4) of 587 Specimens from Three Countries.

Source	d.f.	S.S.	M.S.	F.
Samples	586	1.711		
Country Means	2	.724	.362	212.9*
Error	584	.987	.0017	

*Significant at 1% level.

TABLE IV. T-test and Coefficient of Difference for Antennal Segments Three and Four (X3/X4) Between Countries.

Country	t	Coefficient of Difference	Nonoverlap Per Cent	d.f.
Canada vs. Great Britain	44.5*	1.894	100	543
Canada vs. Japan	3.9*	.231	<75	471
Great Britain vs. Japan	22.4*	3.083	100	157

*Significant at .1% level.

The histogram (Fig. 6) shows how the British population differs from the Canadian and Japanese, and also the homogeneity of the British population: in only two instances was the fourth segment longer than the third. The heterogeneity of Canadian and Japanese populations is apparent.

The correlation coefficients were calculated by plotting the index of the third and fourth segments of the antennae against the total length of segments three and four. The correlation coefficient for Canada was negative and significant (P<.01), indicating a fairly strong relationship of the ratio in this character; for Japan it was negative but showed no significance, indicating a much weaker relationship of the ratio used; and for Great Britain no coefficient was calculated as some of the ratios were less than one. It was impossible to calculate either a regression coefficient or a regression line for the British population for this same reason. Regression lines for Canada and Japan show that any increase in the total length of antennal segments three and four is accompanied by a decrease in the ratio of these segments to one another.

USE OF ANTENNA AND COSTA PLUS STIGMA INDEX

The length of the antenna (X5) and the total length of the costa plus stigma (X6) were measured from 400 antennae and wings respectively of *P. erichsonii* (Fig. 4) from Canada, 108 from Great Britain and 34 from Japan.

As with the two previous characters the analysis of variance (Table V) showed the difference of the samples between countries to be highly significant (P<.01). The t-test (Table VI) also showed that the difference between any two countries was highly significant (P<.001), and of much the same order as with the index of the antennal segments. Application of the coefficient of difference (Table VI) indicated that the nonoverlap between

Canada and Great Britain was 93 per cent, and therefore was sufficiently high to separate these two populations; that between Great Britain and Japan was 100 per cent, with no possibility of error in placing the specimens; and that between Canada and Japan was less than 75 per cent, and therefore was not sufficiently high to separate these two populations with accuracy.

TABLE V. Analysis of Variance of Antenna and Costa plus Stigma (X5/X6) of 542 Specimens from Three Countries.

Source	d.f.	S.S.	M.S.	F.
Samples	541	1.760		
Country Means	2	.916	.458	286.3*
Error	539	.844	.0016	

*Significant at 1% level.

TABLE VI. T-test and Coefficient of Difference for Antenna and Costa plus Stigma (X5/X6) Between Countries.

Country	t	Coefficient of Difference	Nonoverlap Per Cent	d.f.
Canada vs. Great Britain	32.2*	1.49	93	506
Canada vs. Japan	14.2*	.627	<75	432
Great Britain vs. Japan	26.8*	1.914	100	140

*Significant at .1% level.

Attempts to calculate the relationships of the components of this character were not too successful. No correlation or regression coefficients could be calculated for either Canada or Japan, as many of the ratios in this character were less than one. The correlation coefficient for Great Britain was significant ($P < .01$) indicating a strong relationship between the index (X5/X6) and the antennal length (X5). The regression line for Great Britain is useful as it is positive and, though the deviation from linearity is not too great, it showed that any increase in the total length of the antenna was associated with an increase in the ratio of antennal length to the total length of costa plus stigma.

USE OF THE MEDIAN FOVEA

The character of the median fovea (Fig. 1, *mf*) is neither countable nor measurable; therefore the following four descriptive classes were set up.

(1) Fovea pear-shaped; basal depression very deep, in the form of a cone and extending apically as a long furrow, the apex of which is usually tapered and sometimes breaks ridge of frontal crest.

(2) Fovea oval; basal depression shallow with broad bottom and often with a central elevation; apical furrow shallow, rounded, broad, and very short; furrow not tapered apically and never reaches ridge of frontal crest.

(3) Fovea oval or irregular rectangular; basal depression kidney-shaped or ellipsoidal (if rounded then very small) and deep; apical furrow shallow, rounded or rectangular, and broad; furrow not tapered apically and never reaches ridge of frontal crest.

(4) Similar to (3) except apical furrow, or at least its midline, breaks ridge of frontal crest.

After examination, 661 specimens from Canada, 45 from Great Britain, and 40 from Japan were placed in these classes.

All the British specimens fell into (1), those from Canada fell into (2) and (3), with the exception of three specimens which fell into (4), and those from Japan fell into (4). As there was no overlap between the British and Canadian and the British and Japanese specimens the differences were highly significant. A chi-square test was applied to the specimens from Canada and Japan, where a small overlap occurred, and the difference was found to be highly significant ($X^2 = 156.6$; $P < .001$). In using this character too the hypothesis that the samples were all drawn from the sample population is disproven.

GENERAL DISCUSSION

There was no possibility of showing morphological correlates of resistance or susceptibility to encapsulation in the sawfly populations from Great Britain and Canada, because of Maw's findings in 1955. The results of the morphological study, however, showed a clear taxonomic separation of the populations from Great Britain, Canada, and Japan.

The pentagonal area index was the most important character as it allowed the immediate separation of the three populations with no overlap in the samples studied. The remaining characters were of secondary importance, though they did allow the separation of the British population from both the Canadian and Japanese populations.

The Canadian and Japanese specimens are more difficult to distinguish from each other on the basis of the characters of secondary importance. In this regard, extreme caution must be observed in interpreting the results of the analysis of variance and t-test for variations between countries. The F and t values for the two measurable characters (third and fourth antennal segments, antennal length and length of costa plus stigma) indicated a highly significant difference between the sample populations from the three countries. The magnitude of the difference between Canada and Japan, though significant, was less than that between any other two of the countries. The application of the coefficient of difference for both characters illustrated the close affinity of these two populations. The nonoverlap per cent was less than 75, which meant that it was impossible to separate 90 per cent of the Canadian sawflies from 90 per cent of the Japanese sawflies with any degree of accuracy. In the character of the median fovea, however, a simple chi-square test showed a significant difference between specimens from these two countries even though a very small overlap occurred.

A key for the separation of the sawflies from the three geographically isolated areas was prepared, utilizing the characters reviewed above.

Key to Adult Females of *P. erichsonii* from Great Britain, Canada, and Japan:

1. Pentagonal area twice as wide as long; antennal segments three and four equal in length; antenna longer than costa plus stigma; median fovea pear-shaped in outline, the circular depression deep and in the form of a cone, its extension deep, narrow, and pointed apically. . . . . British Population

   Pentagonal area more than twice as wide as long; third segment of antenna longer than fourth; antenna usually shorter than costa plus stigma; median fovea oval or rectangular in outline, the basal depression more or less kidney-shaped, its extension shallow, broad, and not pointed apically. 2

2. Pentagonal area two and a half times as wide as long; frontal crest not broken by median fovea. . . . . Canadian Population

   Pentagonal area three times as wide as long; frontal crest broken by median fovea. . . . . Japanese Population

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REFERENCES

Benson, R. B. 1952. A new *Anoplonyx* destructive to larch in Britain (Hymenoptera: Tenthrediniae). *Bull. Ent. Res.* 43: 543–547.

Cameron, P. 1885. A monograph of the British phytophagous Hymenoptera. Vol. 2: 233 pp. *The Ray Society*, London.

Cresson, E. T. 1880. Description of new North American Hymenoptera in the collection of the Entomological Society. *Trans. Am. Ent. Soc.* 8: 7.

Dobrodeiev, A. I. 1921. Bolshoi Listvennitsknoi Pililshtskik [In Russian]. *In* Reports of the Applied Entomological Section of the Agricultural Research Committee, 1: 100–128. Peterburg, Russia.

Enslin, E. 1912–1918. Die Tenthredinoidea Mitteleuropas. *Beih. Deut. Ent. Z.*, 1912–1917: 790 pp.

Hewitt, C. G. 1912. The large larch sawfly (*Nematus erichsonii*) with an account of its parasites, other natural enemies and means of control. *Canada, Dept. Agr., Ent. Bull.* 5: 42 pp.

MacGillivray, A. D. 1917. Tenthredinoidea. *In* The Hymenoptera or wasp-like insects of Connecticut. Guide to the insects of Connecticut. Part III. *Connecticut Geol. Nat. Hist. Surv. Bull.* No. 22 (1916): 824 pp.

Marlatt, C. L. 1896. Revision of the Nematinae of North America, a sub-family of leaf-feeding Hymenoptera of the family Tenthredinidae. *U. S. Dept. Agr., Div. Ent., Tech. Series* No. 3: 135 pp.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology. *McGraw-Hill Book Co. Inc.*, New York, Toronto, London.

Muldrew, J. A. 1955. Parasites and insect predators of the larch sawfly. *Canadian Ent.* 87: 117–120.

Packard, A. S. 1890. Insects injurious to forest and shade trees. Fifth Report of the United States Entomological Commission, being a revised and enlarged edition of Bulletin No. 7, U.S. Dept. Agr., 928 pp.

Zur Färbungsvariation be *Formica truncorum* Fab.

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EINLEITUNG

Bekannt ist dass die Färbung des Kopfes, der Brust und der Gaster bei den zu der Untergattung Formica *Forel gehörenden Arten individuellen Veränderlichkeiten unterworfen ist, die zur Aufstellung einiger Varietäten führte. Hierzu erwähnt Stitz (1939) dass diese zur Gruppe* rufa *gehörenden Varietäten oft nicht scharf abzugrenzen sind, namentlich wenn es sich um die Bestimmung vereinzelter Tiere handelt, und dass häufig dieselben mit den Bewohnern mit typischen Merkmalen in demselben Nest vorkommen.*

Dies veranlasste mich, die individuelle Variation in der Färbung auf Grund eines reichlichen Materials bei einer zur Gruppe Formica rufa *L. gehörenden Art einer analytischen Untersuchung zu unterziehen.*

Einleitend sei erwähnt, dass die einzelnen von mir aufgestellten Variationstypen der Färbung mit Namen bezeichnet wurden, nicht, um die Systematik zu erschweren, sondern ausschliesslich um die Bezeichnung der Färbungsunterschiede zu erleichtern, was durch Buchstaben oder Ziffern nicht in dem gewünschten Masse hätte erreicht werden können. In diesem Sinne wünsche ich, dass die neueingeführte Nomenklatur aufgefasst werde.

Im Folgenden sollen die Ergebnisse meiner Untersuchungen an Formica truncorum *Fab. (=* F. truncicola *Nyl.) gegeben werden.*

Die zur analytischen Untersuchung dienenden Tiere dieser Art stammten aus einem bei Sinaia (reg. Ploesti), in einer Höhe von ungefähr 1400 m befindlichen Nest. Dasselbe befand sich in einem hohen Baumstumpf einer Buche, am Rande eines Mischwaldes mit vorherrschenden Buchen (*Fagetum abietosum*). Zur Untersuchung gelangten nur Arbeiter, da keine Männchen und nur 4 Weibchen gefunden wurden.

Aus dem Schrifttum einschlägiger Werke ist zu ersehen, dass bei dieser Ameisenart die Färbung des Kopfes, der Brust und der Gaster ziemlich veränderlich ist. Nach Mayr (1861) ist die Farbe der Tiere hellrot, der Hinterleib aber, mit Ausnahme der vorderen Hälfte des ersten Segmentes, braun; Kopf selten mit einem braunen Fleck. André (1882) erwähnt über die Färbung der Tiere: "d'un ferrugineux clair. Funicule des antennes et abdomen (sauf le devant du premier segment), parfois aussi une petite tache sur le vertex d'un brun noirâtre. Chez les petits individus, les teintes brunissent, se confondent et il devient difficile de les distinguer de l'espèce suivante (*Formica pratensis* de Geer)". Aehnlich sind die Angaben von Bondroit (1918): "Corps d'un brun roux assez clair, gastre d'un gris brun foncé, sauf la basse, front souvent rembruni". Nach Stitz (1930) sind die Tiere dieser Art rostrot, jedoch die Fühlergeissel und Hinterleib, mit Ausnahme der Basis des 1. Segmentes, zuweilen auch ein kleiner Fleck auf dem Scheitel schwarzbraun. Ausführlicher ist Stitz (1939) in seiner monographischen Arbeit über die Ameisen Deutschlands, daselbst befinden sich folgende Angaben: "Kopf, Fühler und Thorax von hellem Ziegelrot bis Dunkelrot. Mandibeln und distale Hälfte der Fühlergeissel mitunter braun, der Scheitel, besonders bei kleinen Arbeiter, in der Mitte zuweilen leicht gebräunt oder mit einem bräunlichen Fleck, ebenso Pronotum und Mesonotum. Gaster dunkelbraun, das 1. Segment vorn mehr oder weniger ausgedehnt rot, mitunter die ganze Gaster rötlich mit dunklen Segmenträndern". Die Arbeiter der 1. Generation sollen nach Wasmann im ganzen meist ziemlich dunkel sein. Stitz bringt einige von Krausse, Forel und Emery aufgestellte Varietäten.

Im Anschluss an diese Aufzeichnungen werden weiter unten die Ergebnisse meiner Untersuchungen in Kürze gegeben, indem die Färbungsvariationen des Kopfes mit denen des Thorax und der Gaster vergleichend in Beziehung gebracht werden.

DIE VARIABILITÄT IN DER FARBUNG DES KOPFES

In der Färbung des Kopfes konnten 8 Formen festgestellt werden, und zwar:

1. *Forma ferruginea.*—Der ganze Kopf ziegelrot bis dunkelrot gefärbt, nur die Mandibeln und die seitlichen Spitzen des Clypeus dunkelbraun bis schwärzlich.

2. *Forma fuscobipunctata.*—Wie *forma ferruginea* nur in der Gegend der Punktaugen zwei braune Punkte.

3. *Forma fuscomaculata.*—Die beiden Punkte in der Gegend der Punktaugen verschmolzen, bilden einen grossen braunen Fleck.

4. *Forma fuscifrons.*—Die Stirn von den Punktaugen bis zum Stirnfeld braun, ohne den inneren Rand der Netzaugen zu berühren.

5. *Forma rufocinctuta.*—Die braune Färbung der Stirn dehnt sich über das Hinterhaupt aus, doch in der Gegend der Punktaugen durch eine rote Binde unterbrochen.

6. *Forma fusco—rufocinctuta.*—Wie *forma rufocinctuta*, nur dehnt sich die braune Färbung der Stirn bis zur Mitte des Innenrandes der Netzaugen aus.

7. *Forma rufomaculata.*—Stirn bis zur Mitte des Innenrandes der Netzaugen und das Hinterhaupt braun, am Scheitel jedoch ein rötlicher Fleck.

8. *Forma planefusca.*—Stirn bis zur Mitte des Innenrandes der Netzaugen, Scheitel und Hinterhaupt dunkelbraun.

Von diesen 8 Färbungsformen war *f. ferruginea* am häufigsten vertreten (50%) und kann somit als typische Form angesehen werde; *f. fuscifrons* auch ziemlich häufig (15%), ihr folgten *f. fuscobipunctata* und *f. fuscomaculata;* die anderen Färbungsformen nur in einem geringeren Prozenstatze, von diesen aber *f. planefusca* am zahlreichsten.

DIE VARIABILITÄT IN DER FÄRBUNG DES THORAX

In der Färbung des Thorax konnten 6 Formen festgestellt werden und zwar:

1. *Forma ferruginea.*—Der ganze Thorax ziegelrot oder dunkelrot.

2. *Forma fuscimesonotum.*—In der Mitte des Mesonotum ein brauner Fleck, der nicht den Vorderrand des Scutellums berührt.

3. *Forma mediofusca.*—Wie *f. fuscimesonotum*, doch die vordere Hälfte des Scutellum braun.

4. *Forma fusciscutellum.*—Scutellum und Epinotum ganz braun.

5. *Forma basifusca.*—Epinotum braun, Scutellum nur am Grunde braun.

6. *Forma planefusca.*—Der ganze Thorax braun.

Von diesen 6 Färbungsformen war *f. ferruginea* am häufigsten vertreten (80%), einen hohen Prozentsatz zeigt auch *f. basifusca* (14,7%); die anderen Formen sind seltener.

DIE VARIABILITÄT IN DER FÄRBUNG DER GASTER

In der Färbung der Gaster konnten 5 Formen festgestellt werden, und zwar:

1. *Forma semirufa.*—1. Segment schwarzbraun, in der vorderen Hälfte jedoch rot.

2. *Forma rufomarginata.*—1. Segment schwarzbraun, nur der Vorderrand rot.

3. *Forma nigroproducta.*—1. Srgment in der vorderen Hälfte rot, die schwarzbraune Hälfte im roten Felde schmal vorgezogen.

4. *Forma rufoangulata.*—1. Segment schwarzbraun, die Vorderecken rot.

5. *Forma nigra.*—1. Segment ganz schwarzbraun.

Von diesen 5 Formen war *f. nigra* am häufigsten (47%), die anderen Formen zeigten einen Prozentsatz zwischen 10, 5-20. In sehr geringer Anzahl *f. nigroproducta* (3,7%).

Werden alle beobachteten Färbungsvariationen einer näheren Betrachtung unterzogen, so ist erstens ersichtlich, dass die einheitliche ziegelrote oder dunkelrote Farbe des Kopfes und des Thorax vorherrschend ist (50% und 80%) und bei der Gaster die einheitliche schwarzbraune (47%). Diese Farben an den drei Körperteilen gleichzeitig auftretend (*f. ferruginea* + *f. ferruginea* + *f. nigra*) ergeben eine Färbung des Körper die als nominativ bezeichnet werden kann und dieses ist auch aus dem einschlägigen Schrifttum zu ersehen.

In der Färbung jeder der drei Körperteile tritt anderseits ein progressiver nomischer Pigmentierungsprozess auf, eine Variationsreihe des Braunwerdens, durch welche die weiter oben erwähnten Färbungsformen entstehen. Diese nomischen Variationen in der Färbung der einzelnen Körperteile (Kopf, Thorax, Gaster) entwickeln sich verschieden und durch Anordnung derselben entsteht eine Reihe verschieden gefärbter Tiere, bei welchen jedoch keine morphologischen Unterschiede festgestellt werden konnten, wie z.B. in der Behaarung des Fühlerschaftes, der Schienen, des Kopfes, der Augen oder des Thorax.

Die Färbungsvariationen des Körpers der Tiere im ganzen betrachtet, lassen auch eine gerichtete Gesetzmässigkeit ersehen, die sich in einer nomischen Neigung zur Braunfärbung äussert. Die Tiere mit dunkelbraun gefärbten Kopf zeigen auch in der Thorax—und Gasterfärbung dunklere Farben. Als Regel dürfte dies vielleicht nicht gelten. Weitere Untersuchungen werden Klarheit darüber geben.

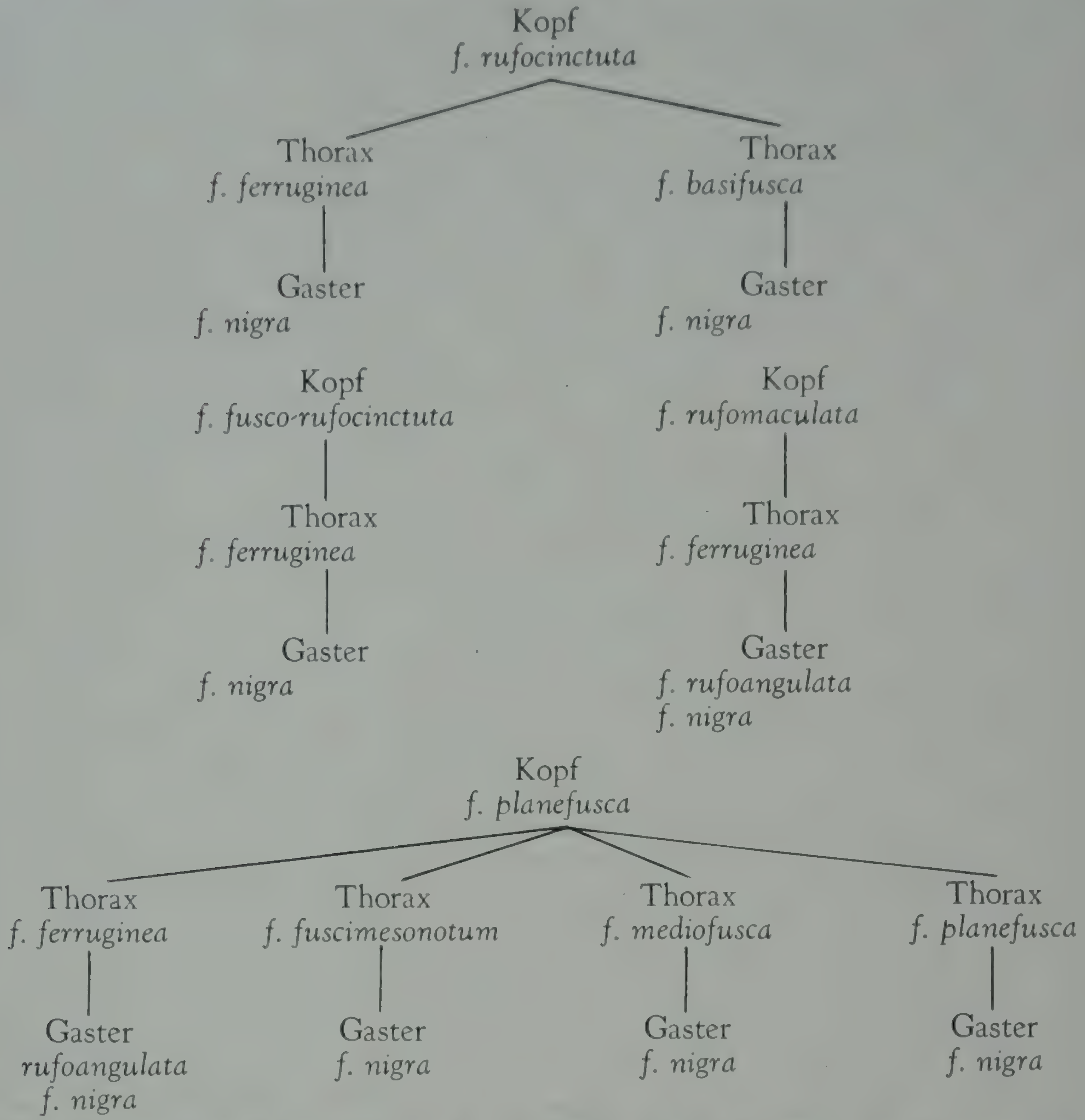
Im ganzen sind 39 Färbungsvariationen in dem aus 265 Tieren bestehenden Untersuchungsmateriale gefunden worden und diese in ein System geordnet, stellen sich folgendermassen dar:

- Kopf *f. ferruginea*
  - Thorax *f. ferruginea*
    - Gaster
      - *f. semirufa*
      - *f. rufomarginata*
      - *f. nigroproducta*
      - *f. rufoangulata*
      - *f. nigra*
  - Thorax *f. basifusca*
    - Gaster
      - *f. semirufa*
      - *f. rufomarginata*
      - *f. nigroproducta*
      - *f. rufoangulata*
      - *f. nigra*
  - Thorax *f. fusciscutellum*
    - Gaster
      - *f. marginata*
      - *f. rufoangulata*
      - *f. nigra*

- Kopf *f. fuscobipunctata*
  - Thorax *f. ferruginea*
    - Gaster
      - *f. rufomarginata*
      - *f. rufoangulata*
      - *f. nigra*
  - Thorax *f. basifusca*
    - Gaster
      - *f. semirufa*
      - *f. rufomarginata*
      - *f. nigra*

- Kopf *f. fuscomaculata*
  - Thorax *f. ferruginea*
    - Gaster
      - *f. rufoangulata*
      - *f. nigra*
  - Thorax *f. basifusca*
    - Gaster
      - *f. semirufa*
      - *f. rufomarginata*
      - *f. rufoangulata*
      - *f. nigra*

- Kopf *f. fuscifrons*
  - Thorax *f. ferruginea*
    - Gaster
      - *f. semirufa*
      - *f. rufomarginata*
      - *f. rufoangulata*
  - Thorax *f. basifusca*
    - Gaster
      - *f. rufoangulata*


Kopf
f. rufocinctuta
Thorax
f. ferruginea
Gaster
f. nigra
Thorax
f. basifusca
Gaster
f. nigra
Kopf
f. fusco-rufocinctuta
Thorax
f. ferruginea
Gaster
f. nigra
Kopf
f. rufomaculata
Thorax
f. ferruginea
Gaster
f. rufoangulata
f. nigra
Kopf
f. planefusca
Thorax
f. ferruginea
Gaster
rufoangulata
f. nigra
Thorax
f. fuscimesonotum
Gaster
f. nigra
Thorax
f. mediofusca
Gaster
f. nigra
Thorax
f. planefusca
Gaster
f. nigra

Die festgestellten Unterschiede in der Färbung des Kopfes, des Thorax und der Gaster veranschaulichen die Breite der individuellen Variation innerhalb der Bewohner eines Nestes. In der Zusammensetzung der Färbungsvariationen dürften noch weitere Formen auftreten; zukünftige Untersuchungen werden Aufschluss darüber bringen.

Die von Krausse aufgestellten Varietäten *menozzi*, *finzii*, *stitzi* und *staegeri* sind vielleicht nur Formen individueller Variation. Die kurzen Diagnosen dieser 4 Formen erlauben nicht dieselben mit Sicherheit im obigen System einzureihen. Die Varietäten *truncicola—pratensis* Forel und *dusmeti* Emery besitzen in der Behaarung der Augen, des Fühlerschaftes, des Thorax und des Kopfes einige morphologische Unterschiede gegenüber der Nominatform, und können somit als Varietäten angesehen werden.

LITERATURVERZEICHNIS

André, E. 1882. Spéciès des Hymenoptères d'Europe et d'Algérie. Vol. II. Baune.
Bondroit, J. 1918. Les fourmis de France et de Belgique. *Ann. Soc. Entom. de France.* 87: 1–174.
Mayr, G. 1861. Die europäischen Formiciden. Wien.
Stitz, H. 1930. In Schmiedeknecht, O. Die Hymenopteren Nord—und Mitteleuropas. Jena, pp. 521–563.
Stitz. H. 1939. Die Tierwelt Deutschlands, Formicidae. Jena.

DISCUSSION

W. L. Brown, Jr. Variations of *Formica truncorum* may be found in one nest. In the North American *truncorum* group, mixed nests of different species are frequently formed (between at least 3 species). This results in mixed workers.

W. K. Knechtel. Tous les exemplaires des fourmis étudiées ont été pris dans un même nid (265 individus) et les descriptions de la couleur de la tête, du thorax et de l'abdomen ont été faites uniquement d'après ceux-ci. Des observations sur la couleur des femelles n'ont pas été faites, à cause du manque de femelles (seulement 4 exemplaires ont été trouvés dans ce nid).

Phylogenetic Relationships within the Genus *Osmia* (Hymenoptera: Megachilidae) in the New World[1]

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ABSTRACT

A study of 138 species (approximately 20,000 specimens) has been made to postulate the interrelationships of 11 subgenera of Osmia. *Of these* Diceratosmia, Nothosmia, Chenosmia, *and* Euthosmia *are found to be most generalized subgenera. Each of the generalized subgenera has given rise to at least one specialized subgenus. Although* Diceratosmia *is the central stock from which common stocks of other subgenera branch out,* Acanthosmioides *arises from* Nothosmia, Cephalosmia *from* Euthosmia, Centrosmia *from* Chalcosmia, *and* Monilosmia *from* Chenosmia. *The two highly specialized subgenera,* Osmia *and* Trichinosmia *(monotypic) are of questionable relationship. These are supposed to have arisen directly from* Diceratosmia *stock. A brief account of the distribution of the species groups are given along with comments on nearly 70 Old World species.*

The purpose of this paper is to present the phylogenetically significant characters of the American subgenera of leaf-cutting and solitary bees of the genus *Osmia* and to discuss interrelationships of these subgenera. A problem of this nature is difficult to solve in case of a genus such as *Osmia* which includes a large number of Old World species, about which there is doubt as to the taxonomic position, and to which the author did not have access.

Of approximately 211 species studied, 138 occur in the New World. The rest are from the Old World and only a small fraction of the latter belong within the genus *Osmia* as defined by American authors (Michener, 1941). The number of subgenera occurring in the New World are eleven in all. Of these the subgenus *Trichinosmia* is monotypic (Sinha, 1955).

The morphological terminology used in this study is mainly from Michener (1944). In the female there are three or four teeth. These are counted in the following order: tooth 1, the uppermost; tooth 2; tooth 3; tooth 4, the lowermost. The second tooth is often small, rudimentary, almost confluent with the first or even absent in certain subgenera. The width of the hind basitarsus is measured at the point of the maximum width. A distinction has been made between the abdominal and the metasomal tergum and the sternum. Morphologically, the first metasomal tergum is the second abdominal segment or the one posterior to the propodeum.

For the purposes of discussion the eleven subgenera of the genus *Osmia* are placed into three major categories. In the first category are the four most generalized subgenera (*Diceratosmia*, *Nothosmia*, *Chenosmia*, and *Euthosmia*). In the second category are five of the more specialized subgenera (*Chalcosmia*, *Centrosmia*, *Acanthosmioides*, *Cephalosmia*, and *Monilosmia*) which are clearly derived from the generalized subgenera. The third category consists of two highly specialized subgenera (*Osmia* and *Trichinosmia*) of questionable relationships. It should be emphasized that the phylogenetic relationships postulated below may be radically changed after the large number of the Old World species of the genus have been more thoroughly studied.

METHODS

The primitiveness and the degree of modification of certain structures have been used as criteria for determining the inter-relationships of the subgenera. Of approximately one hundred characters utilized in the subgeneric descriptions of both sexes, twenty-nine were selected for the study of phylogenetic relationships. Each of these characters was chosen because the alternative condition that was primitive and the alternative condition that was derived could be decided by comparison with the alternative conditions of the same character in less specialized genera of the tribe Megachilini,[3] subfamily Megachilinae

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[1] Parts of this paper are incorporated in an enlarged paper in the *Univ. Kansas Sci. Bull.* (In press).

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[3] According to the recent classification (Michener, 1944: 256–268; Hurd and Michener, 1955: 6–10) the family Megachilidae includes only two subfamilies, Lithurginae and Megachilinae. The genus *Osmia* is placed in the tribe Megachilini of the subfamily Megachilinae.

(see Michener, 1941: 151). On this basis two or more alternative conditions of each selected character are listed below. The characters in the left column are considered to be primitive because of agreement with the characters of various generalized genera of Megachilini, whereas those in the right hand column are judged to be derived since characters differ from those in the genera considered as generalized.

A method of ascertaining the relation of one subgenus to another is as follows: For a given structure, decide what character (color, size, shape or number of parts) is primitive. Note which subgenus has derived characters. If all species of the first subgenus are specialized and if some species of the second subgenus are specialized and if the rest of the species are generalized, the second subgenus possibly is ancestral to the first. If the other characters are in concordance, the possibility becomes a probability. Closeness of relationship between members of a pair of subgenera is estimated by the number of characters common to the two subgenera. Although two subgenera may have a number of common characters, another pair of subgenera with the same number of characters in common may have many more contrasting characters. The more such contrasting characters there are, other things being equal, the less probably there is of close relationship.

In the discussion of the relationship that follows the words "primitive," "derived," and "modified" are used to describe the condition of the morphological features. The words "generalized" and "specialized" are used to describe the condition of species, a group of species or a subgenus in reference to all of the features studied. For instance, a subgenus is generalized if it has a large number of primitive characters and specialized if it has a large number of derived characters.

Identical "derived" characters in some species of each of two subgenera, but not in all species of either, are regarded as another indication of probable relationship between the two subgenera concerned, except in instances where it is judged that there has been parallel evolution in two unrelated or distantly related subgenera in response to similar environmental conditions.

PHYLOGENY

In postulating the phylogenetic arrangement of the genera of Osmiinae,[4] Michener (1941: 151) assumed rightly that those Osmiini[4] having characteristics most nearly similar to the various short-tongued bees and wasps were the most primitive. On the basis of this assumption *Chelostoma* and *Prochelostoma* were found to most nearly approach the primitive type because the two mentioned genera have the longest notalices found in the group, an elongate thorax with the anterior parts of the propodeum horizontal, and large pterostigmata. According to him, the genus *Osmia*, with punctiform notalices (parapsidal lines), is one of the most specialized genera of the subfamily Osmiinae. Various other characters supported this conclusion. *Diceratosmia* (a genus according to his classification) has the shortest parapsidal lines of all the more generalized genera and thus was placed immediately below *Osmia* in the phylogenetic tree. A careful examination has revealed extremely short parapsidal lines in *Osmia marginata* Michener, a desert species of *Nothosmia*. This species seems to be a connecting link between the generalized *Dicheratosmia* and the slightly more specialized *Nothosmia*. All species of *Diceratosmia* possess a distinct carina along the inner ventral angle of each posterior coxa. Such a carina is represented in *marginata* and in O. (*Chenosmia*) *caulicola* in the form of a weak line. This carina probably indicates primitiveness. The carina persists in stronger from in some of the most generalized genera of the Megachilinae such as *Prochelostoma*, *Heriades*, *Noteriades*, and *Proteriades*. The carina is absent in *Hoplitis*, but manifests itself in all forms of intergradation from a fairly conspicuous carina to a feeble line in the genus *Anthocopa*, which is comparatively less primitive in other characters than the previously mentioned genera. *Diceratosmia submicans* Morawitz (Egypt) strikingly resembles *marginata* of *Nothosmia* from the desert areas of California in having extremely short parapsidal lines and weak or evanescent carinae on the hind coxae. Therefore, *Diceratosmia* seems to be the most generalized group of the genus and *Nothosmia* is a close relative which is also generalized and probably derived from the former early in the history of the genus.

Diceratosmia retains twenty-eight of the twenty-nine primitive characters listed in Table I. The only modification is the quadridentate condition of the mandible of the female.

[4] The subfamily name Osmiinae and the tribe name Osmiini are not used in more recent classifications (Michener, 1944: 256-268; Hurd and Michener, 1955: 6-10) in which the groups are included in the tribe Megachilini. However, it denotes a natural assemblage of non parasitic megachilids having arolia.

TABLE I. Primitive and Derived Characters in the Genus *Osmia*.

No.	Primitive	Derived
1.	Size small	Size large
2.	Pubescence white or pale, of median length	Pubescence dark or black, long or short
3.	Mandible of female with three teeth	Mandible of female with four teeth
4.	Mandible of male: angle of tip of upper tooth right angle or acute	Mandible of male: angle of tip of upper tooth obtuse
5.	Mandibular constriction moderately wide	Mandibular constriction narrow, or absent and entire mandible broad
6.	Mandible of female lacking transverse ridge or protuberance near base	Mandible of female having transverse ridge or protuberance
7.	Malar space absent	Malar space present
8.	Genal area of female lacking depression immediately below eye	Genal area of female with a round or elongate depression
9.	Genal area of female unequal to width of eye	Genal area of female significantly wider or narrower* than eye
10.	Inner margins of eyes converging anteriorly	Inner margins of eyes parallel or diverging anteriorly
11.	Clypeus of female lacking apical margin; not swollen or unmodified	Clypeus of female having apical margin swollen or otherwise modified
12.	Clypeal punctations of female nearly confluent	Clypeal punctations of female widely separated or confluent
13.	Clypeal margin of male having impunctate band of moderate width	Clypeal margin of male having or lacking narrow impunctate band
14.	Hypostomal carina of female low	Hypostomal carina of female high, abruptly reduced behind angle, forming a tooth
15.	Antennal socket having margin uniform throughout	Antennal socket having superior-masal margin higher than remaining margin
16.	Flagellar segments of antennae in male unmodified (cylindrical, about 1.5 times as long as wide)	Flagellar segments of antennae in male modified (moniliform, or last segment compressed and expanded, or each segment twice as long as wide)
17.	Hind coxa with a ventral carina	Hind coxa without a ventral carina
18.	Mediotarsal segments of middle leg not swollen	Mediotarsal segment of middle leg greatly swollen
19.	Strigilis of male having malar spine not greatly produced	Strigilis or male having malar spine greatly produced
20.	Basitarsus of hind leg of male lacking tooth	Basitarsus of hind leg of male having tooth
21.	Forewing: hairs of cells short	Forewing: hairs of cells long
22.	Middle femur of male lacking a projection on lower side	Middle femur of male having a projection on lower side
23.	Hind basitarsus of male parallel-sided	Hind basitarsus of male modified (wider towards base, at apex or middle)

*Possibly the primitive condition.

TABLE I. *Continued*

No.	Primitive	Derived
24.	Metasomal terga of male with moderately wide impunctate band	Metasomal terga of male with or without narrow or wide impunctate band
25.	Metasomal sternum 2 of male lacking posterior tooth	Metasomal sternum of male having posterior tooth
26.	Gonocoxite of male(having weak subapical swelling	Gonocoxite of male lacking subapical swelling
27.	Subapical hairs on gonocoxite of male diffuse	Subapical hairs on gonocoxite of male forming a tuft
28.	Gonocoxite of male lacking a subapical process	Gonocoxite of male having a subapical process
29.	Penis valve of male lacking long ventral longitudinal groove	Penis valve of male having long, ventral longitudinal groove

Nothosmia retains only twenty-seven primitive characters and is specialized in two, namely, in having a tooth on the hind basitarsus in some males and in having the impunctate apical bands on the metasomal terga of the male narrow.[5] A common tendency towards mandibular constriction among the females of a few species of each subgenus supports the idea of close relationship of these two generalized subgenera.

The third most generalized subgenus is *Chenosmia;* it retains the same number of primitive characters as *Nothosmia* but shares with *Diceratosmia* the derived quadridentate condition of the mandible in the female. The presence of a tooth on the hind basitarsus of the males in some species of *Nothosmia* and the absence of such a tooth in some species of

TABLE II. Twenty-nine Primitive and Derived Alternative Characters Among Subgenera of *Osmia*.

Subgenus	Number of Characters		
	Primitive	Partly derived*	Derived
Diceratosmia	22	6	1
Nothosmia	21	6	2
Chenosmia	23	4	2
Euthosmia	24	1	4
Chalcosmia	17	2	10
Centrosmia	11	8	10
Acanthosmioides	13	4	12
Monilosmia	16	6	7
Cephalosmia	13	7	9
Trichinosmia	18	0	11
Osmia	13	4	12

*Partly derived means specialized in some species, not in others.

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[5] This and the following discussion suggest that there are few subgeneric characters. As the systematic section shows, there are some other characters which, however, could not be included in Table I and hence must be disregarded here.

TABLE III. Relationships of the Subgenera of the Genus *Osmia* Based on Twenty-nine Selected Characters.

Characters Listed in Table I)	Subgenera of Osmia										
	Nothosmia	*Diceratosmia*	*Euthosmia*	*Chenosmia*	*Monilosmia*	*Chalcosmia*	*Cephalosmia*	*Centrosmia*	*Trichinosmia*	*Acanthosmioides*	*Osmia*
1	*	*	*	*	X	X	X	0	X	X	X
2	*	*	*	X	X	*	X	X	X	X	X
3	0	X	*	X	X	X	X	X	X	*	X
4	*	*	*	*	*	*	*	*	*	X	*
5	0	0	*	*	*	*	*	*	*	X	*
6	*	*	*	*	*	X	0	X	*	*	*
7	*	*	*	*	*	*	*	0	*	*	X
8	*	*	*	*	*	*	*	*	*	*	X
9	*	*	*	*	X	0	X	X	*	X	X
10	*	0	*	*	*	0	0	0	*	0	X
11	0	*	*	*	*	X	0	X	X	*	0
12	*	0	X	*	*	*	X	*	*	*	*
13	*	0	*	*	0	X	0	X	*	X	0
14	*	*	*	*	X	X	0	0	X	*	*
15	*	*	*	*	*	*	X	*	*	*	*
16	*	*	*	*	0	*	*	0	*	X	*
17	0	*	X	0	X	X	X	X	X	X	X
18	*	*	*	*	*	*	*	X	*	0	*
19	*	0	X	*	*	X	X	0	X	*	X
20	X	0	*	0	0	X	*	*	*	X	*
21	*	*	*	*	*	*	*	*	*	*	X
22	0	*	X	0	X	*	0	X	*	X	*
23	*	*	*	*	0	*	*	0	X	*	*
24	X	*	*	*	*	*	*	*	X	0	X
25	*	*	*	*	*	*	*	0	*	X	*
26	*	*	*	*	0	X	X	X	X	*	*
27	0	*	0	0	0	*	0	*	X	0	0
28	*	*	*	*	*	*	*	*	*	X	0
29	*	*	*	*	*	*	*	*	*	*	X

* Indicates 'all species generalized'. X Indicates 'all species specialized'.
0 Indicates 'some species specialized and others generalized'.
The subgenus *Trichinosmia* is monotypic and lacks the symbol 0 in the column.

TABLE IV. A Method used in Comparing the Relationship Between two Subgenera. Any one of the Characters listed in Table I may Fall in one of the Nine Catagories and Indicate Relationship or lack of Relationship.

Categories	Subgenus A	Subgenus B	Values
1	All species generalized	All species generalized	Relationship
2	All species specialized	All species specialized	Relationship
3	Some species specialized	Some species specialized	Relationship
4	Some species specialized	All species specialized	Relationship
5	All species specialized	Some species generalized	Relationship
6	All species generalized	All species specialized	No relationship
7	All species specialized	All species generalized	No relationship
8	All species generalized	Some species specialized	Relationship
9	Some species specialized	All species generalized	No relationship

Chenosmia, together with the modification of the apical areas of the terga of the males in *Nothosmia*, indicate that *Chenosmia* did not arise from *Nothosmia*. *Chenosmia* probably arose from some *Diceratosmia*-like form near the point of divergence of *Nothosmia*.

The fourth generalized subgenus is *Euthosmia*; it retains twenty-five primitive characters of the twenty-nine listed in Table I and is specialized in four characters, namely, the sparseness of punctations on the clypeus of the female, greatly produced malar spine of the strigilis, modified hind basitarsus of the male, and absence of the carina on the hind coxa. In the first two characters, some species of *Diceratosmia* are likewise specialized. In the last two characters some species of *Nothosmia* are similarly specialized. These specializations bring *Euthosmia* equally close to *Diceratosmia* and to *Nothosmia*. *Euthosmia* was probably derived from *Diceratosmia* and *Nothosmia*, independently of other subgenera.

Acanthosmioides has as many as twelve derived characters and seems to have arisen from *Nothosmia* rather than from *Diceratosmia* (*Diceratosmia* differs from *Acanthosmioides* in thirteen characters) or *Chenosmia* (*Chenosmia* differs from *Acanthosmioides* in eleven characters). From *Nothosmia*, *Acanthosmioides* differs in only nine characters, and there are no modifications in *Nothosmia* that indicate that *Acanthosmioides* was not derived from that subgenus. Moreover, the tooth on the hind basitarsus of the male, which in itself is a significant modification for a generalized group like *Nothosmia*, occurs in *Acanthosmioides* as well.

Chalcosmia and *Centrosmia* have an equal number of primitive characters and seem to be closely related to each other. Each has the same modifications, and in addition in some species of each subgenus the inner margins of the eyes diverge anteriorly. Because of these common characteristics, the two subgenera seem to be more closely related than either subgenus is to any third subgenus. *Centrosmia* is the more specialized of the two, as indicated by the modification of at least four structures (in some of its species) in which the species of *Chalcosmia* are primitive. Also, a few primitive characters of *Chalcosmia*, such as the abundance of pale white or yellowish hairs on the body and the simple mediotarsal segments of the middle leg of the male, are probably qualitatively even more significant than the derived characters in relating the subgenus to the generalized subgenera, such as *Diceratosmia* and *Nothosmia*. Both *Centrosmia* and *Chalcosmia* have more characters in common than with *Nothosmia*, *Euthosmia* or *Chenosmia*. The generalized subgenus *Diceratosmia* could have given rise to *Chalcosmia*. However, the narrowness or absence of the apical impunctate band on the metasomal terga of the male in *Nothosmia* is a modification not present in *Chalcosmia*. Modifications of structures in *Euthosmia* indicate that it is not ancestral to *Chalcosmia*. The presence of well-separated punctations on the clypeus of the female of *Chalcosmia* is a modified condition that could have been inherited from *Euthosmia*. Therefore, it is logical to suppose that the common ancestor of *Chalcosmia* and *Centrosmia* arose from a *Diceratosmia* (or the *Diceratosmia* stock) somewhere near the point of divergence of *Euthosmia* from the *Diceratosmia* stock, or from Euthosmia itself. This ancestral line in turn split into *Chalcosmia* and *Centrosmia*.

In all of its derived characters (the abundance of black pubescence on the body, the quadridentate mandible of the female, and the absence of a carina on each posterior hind coxa) the generalized subgenus *Chenosmia* closely resembles the more specialized subgenus *Monilosmia*. The direction of specialization of some species of *Chenosmia*, such as from small to large size and from low to high hypostomal carinae in the female, indicates possible relations of *Chenosmia* to *Monilosmia*, in which these characters are strongly developed. Moreover, *Monilosmia* shares sixteen primitive characters with *Chenosmia*, thirteen with *Nothosmia*, and only twelve with *Diceratosmia*. *Monilosmia* shares no derived character (in all its species) with *Diceratosmia* or with *Nothosmia*. The closeness of the relationship between *Monilosmia* and *Chenosmia* is further attested by the males of those two subgenera being almost indistinguishable externally. It is concluded that *Monilosmia* arose from *Chenosmia* which, as previously stated, probably arose from the *Diceratosmia* line early in the history.

In the third category of subgenera, the subgenus *Osmia* preserves the minimum number of primitive characters. The absence of a tooth on the hind basitarsus of the male in *Osmia* is a primitive condition, whereas *Nothosmia* is modified in this respect. At least some species of *Diceratosmia* and *Chenosmia* have this modification. The directions of modification within the subgenus are unexpected if judged by the characters of *Nothosmia*, *Diceratosmia*, *Chenosmia* or *Euthosmia*. Certain modifications (already discussed) of each of the other subgenera, except *Diceratosmia* and *Chenosmia*, similarly seem to prevent any one of them being considered as ancestral stock for the subgenus *Osmia*. It resembles *Chenosmia* in dark hair on the body, black scopa in the female, and the quadridentate mandibles of the female (the latter condition is a modification also in the female of *Diceratosmia*). The broadened apical impunctate band on the clypeus of the male in some species of both *Chenosmia* and *Osmia* also suggests a possible relationship between these two subgenera. It is impossible to judge from these facts which, if any, of the generalized subgenera is directly ancestral to the subgenus *Osmia*. In addition, it was found impossible adequately to compare the subgenus *Osmia* with certain of other more specialized subgenera, namely *Centrosmia*, *Cephalosmia* and *Acanthosmioides*, because it was not possible logically to assume that any one of the three is either more generalized or more specialized than the subgenus *Osmia*. Perhaps, if additional characters can be found in the future, such comparisons will be possible. All that can be said is that *Osmia* probably arose from *Diceratosmia* or *Chenosmia* somewhere near the point of divergence of these two subgenera. More probably the subgenus *Osmia* arose from an extinct ancestor of *Diceratosmia* and *Chenosmia*.

Trichinosmia is another subgenus of uncertain taxonomic position. In the retention of common primitive characters, it is closest to *Chenosmia* and not far from *Nothosmia*. With *Chenosmia*, *Trichinosmia* shares two modifications and with *Nothosmia*, one. *Trichinosmia* is monotypic, and, therefore, it can not have some species with derived characters and some species with primitive characters. As in *Osmia*, the modifications seem to indicate relation to either *Diceratosmia* or *Chenosmia* instead of any one of the generalized subgenera.

Cephalosmia preserves more primitive characters than either *Chalcosmia* or *Centrosmia* and shares more primitive characters with *Euthosmia* than with any other generalized subgenus. The derived characters so shared are the well-separated punctations on the clypeus of the female and the long malar spine of the strigilis of the male. *Cephalosmia* resembles *Chenosmia* in fourteen characters of which two are derived (in which two derived characters *Cephalosmia* also resembles *Monilosmia*). Considering the characters in which only some species are specialized, *Cephalosmia* is equally related to *Chenosmia*, *Diceratosmia*, and *Euthosmia*. But there is no modification in *Euthosmia* that indicates that *Cephalosmia* was not derived from that subgenus (such modifications occur in *Diceratosmia* and *Chenosmia*). Thus *Euthosmia* is probably directly ancestral to *Cephalosmia*.

DISTRIBUTION

The genus *Osmia* is known from the Palearctic, Nearctic, and Ethiopian regions. It is absent from the Indo-Australian and Neotropical regions. The subgenus *Diceratosmia* is known from southern Europe, Asia Minor, North Africa, and probably ranges widely across Asia (Dalla Torre, 1896: 382–415; Michener, 1949: 260–264). In the New World this subgenus is widespread in the southern states and extends southward to Costa Rica. This extensive distribution seems compatible with the generalized nature of the subgenus.

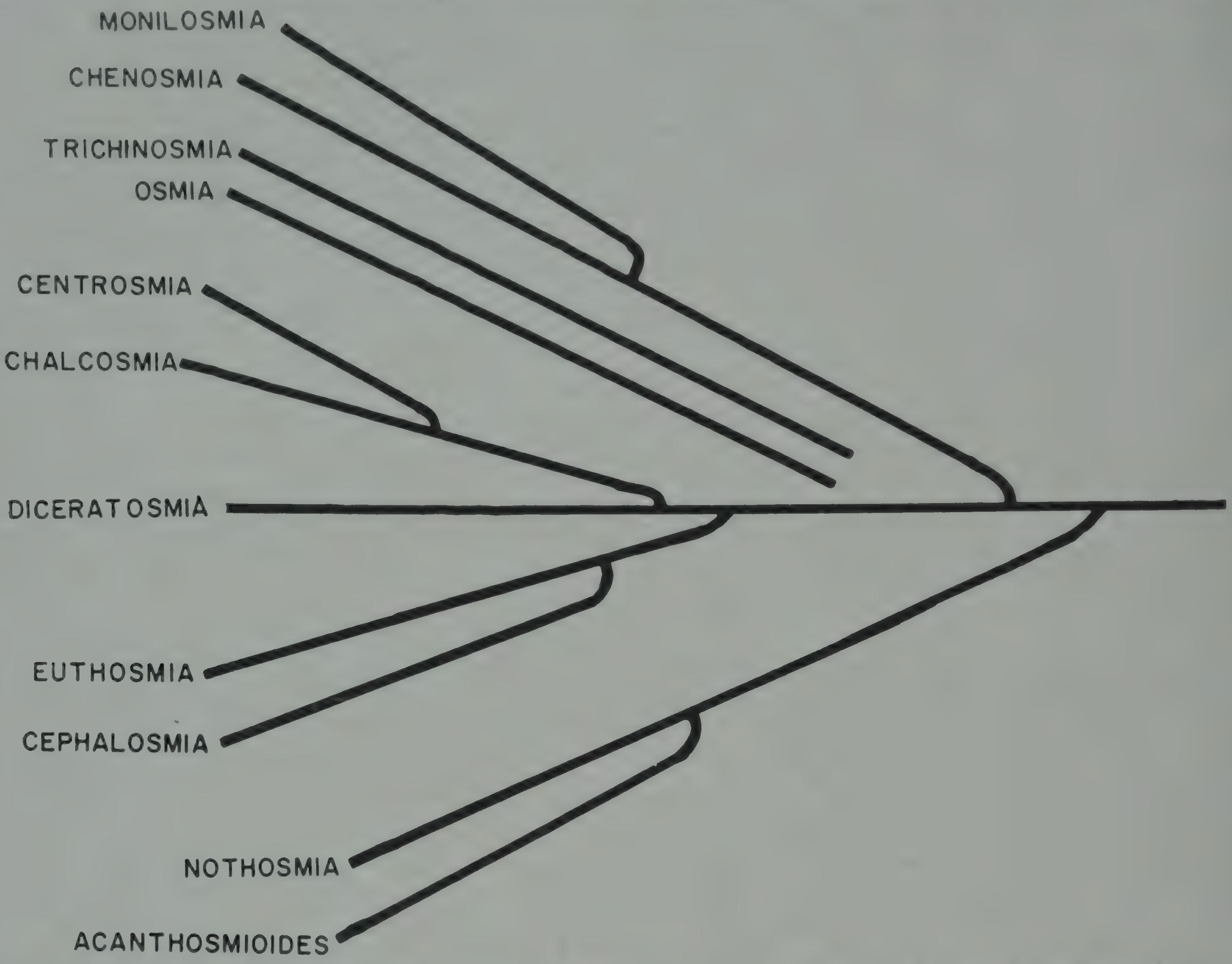

Fig. 1. Phylogenetic scheme showing the probable relationships of the subgenera of *Osmia* Panzer as evolved in the New World.

Diceratosmia is found principally in the southern temperate regions. Hence it likely arose in such climates, perhaps when they extended into northern regions now much cooler, or has been displaced from cooler climates by competition with more specialized subgenera, all of which are more boreal (except *Trichinosmia*, of which there is only one species). This is in agreement with Matthew's hypothesis (1939: 10) that the most advanced groups (he was dealing mainly with higher taxa) should be nearest to the center of dispersal, and the most conservative groups farthest from it. Because the center of dispersal was assumed to be holoarctic, the generalized forms would be expected to be of southern occurrence now.

No species of *Nothosmia* is known from the Old World. In North America that genus occurs from coast to coast but not in cold, montane climates of the west. Species of group I are restricted to the eastern and central parts of North America. Species of group II occur in the desert areas of California and New Mexico. *Acanthosmioides*, a specialized subgenus probably derived from *Nothosmia*, is absent in the Old World and is restricted to mountainous and boreal regions of western North America. Females of *Acanthosmioides* closely resemble the species group II of *Nothosmia*. White (1952: 222) included five of six species of the group II of *Nothosmia* as an aberrant group of *Acanthosmioides*, not having seen the males of any of the species. In the New World, *Diceratosmia* probably gave rise to *Nothosmia* which in turn split into two groups; the predominantly eastern group I remained somewhat generalized, whereas the western group II gave rise to the specialized subgenus *Acanthosmioides*. Perhaps group II of *Nothosmia* has become restricted to the southern deserts because that group could no longer survive elsewhere after the more specialized subgenera arose in country of the kind usually occupied by *Osmia*. This is in accordance with the view that, next to *Diceratosmia*, *Nothosmia* is the most generalized subgenus.

Chenosmia is distributed from coast to coast in North America, but most of the species are in the mountains or boreal regions of the western half of the continent. *Monilosmia*, a closely related stock, is restricted to the western half of North America. The inclusion of *Osmia inermis* and probably of *Osmia nigriventris* extends the known distribution of *Chenosmia* to Eurasia. Although there are many American species of *Chenosmia*, only two European species are known; these are not especially generalized or *Nothosmia*-like Both are far northern, and both are found also in North America. It is likely that they migrated to Eurasia from America in Pleistocene time or in Post-pleistocene time. *Monilosmia*, probably an independent group, arose from *Chenosmia* and remained restricted primarily to the mountainous regions of the western North America.

Chalcosmia is principally Eurasian (see Dalla Torre, 1896: 382–415), having many species and more diversity there than in America; only one species group (plus one introduced European species) occurs in America. The comparatively more specialized subgenus *Centrosmia* is found only in North America and probably originated in this part of the World.

Of the highly specialized subgenera in the third category, the subgenus *Osmia* probably is of Old World origin, as it has a larger number of species and exhibits more diversity there (see Dalla Torre, 1896: 382–415; Yasumatsu and Hirashima, 1950: 3–11); only two species occur in North America. *Cephalosmia* is principally from high altitudes of the western half of North America and is unknown in the Old World. *Trichinosmia* is known from Arizona, Nevada, and California, in semidesert and in forested areas of low elevation.

REFERENCES

Dalla Torre, Karl Wilhelm von. 1896. Catalogus Hymenopterorum; gucusque descriptorum systematicus et synonymicus. Leipzig. Vol. 10, viii+643 pp.

Hurd, Paul D., and Charles D. Michener. 1955. The Megachiline bees of California (Hymenoptera: Megachilidae). *Bull. California Insect Survey* 3: 1–247.

Matthew, W. D. 1915. Climate and evolution. *Ann. N. Y. Acad. Sci. Biol.* 24: 171.

Michener, Charles D. 1941. A generic revision of the American Osmiinae with descriptive notes on Old World genera (Hymenoptera; Megachilidae). *Amer. Midland Nat.* 26: 147–176, 21 figs.

Michener, Charles D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bull. Amer. Mus. Nat. Hist.* 82: 157–326, 246 text figures, 13 diagrams.

Michener, Charles D. 1949. A revision of the American species of *Diceratosmia* (Hymenoptera: Megachilidae). *Ann. Ent. Soc. Amer.* 42: 258–264, 10 figs.

Sinha, Ranendra N. 1955. A subgeneric revision of the bees of the genus *Osmia* in America north of Mexico (Hymenoptera: Megachilidae). Unpublished thesis, University of Kansas.

White, Jimmy R. 1952. A revision of the genus *Osmia*, subgenus *Acanthosmioides* (Hymenoptera: Megachilidae). *Univ. Kansas Sci. Bull.* 35: 219–307.

Yasumatsu, K., and Y. Hirashima. 1950. Revision of the Genus *Osmia* of Japan and Korea (Hymenoptera: Megachilidae). *Mushi* 21: 1–18, 3 pls.

Les Types Provancher, Huard et Autres Collaborateurs, 1869-1896[1]

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RÉSUMÉ

Si on veut l'accord avec les exigences de l'article 21 du Code international de Nomenclature zoologique qui stipule que l'auteur d'un nom spécifique est la première personne qui publie ce nom avec une indication, une définition ou une description, il y aurait alors lieu de reviser certaines paternités de plusieurs espèces que les auteurs ont attribuées à Provancher, à Huard, à Burque, à Brodie, ou à Ashmead.

Bien que l'on sache de façon certaine, par le texte de la publication qu'une personne a contribué partiellement à la description d'une espèce nouvelle en donnant quelques indications, ou, même si la description entière est due à cette même personne, il semblerait inéquitable de lui en attribuer la propriété entière, comme l'exige l'article 21, quand la publication de cette description en est faite par une autre personne trois ou quatre ans après la mort du premier. D'un autre coté, il ne semblerait guère plus équitable d'accorder au responsable de la publication la propriété d'auteur d'un nom spécifique nouveau qu'une autre personne a attribué à une espèce nouvelle en la décrivant en entier ou en plus grande partie; i.e. les espèces de Provancher décrites en 1891 et dont les descriptions sont publiées par Huard dans le Naturaliste Canadien *de 1892 à 1896.*

Le travail de révision d'un groupe assez considérable de lectotypes et la vérification du dernier catalogue synoptique des hyménoptères de l'Amérique du Nord nous amène à constater, sans doute aucun, que l'interprétation rigoureuse de l'article 21 du Code international de Nomenclature zoologique entraine parfois certaines difficultés d'application qui sont à l'origine de plusieurs erreurs commises dans le passé par nombre d'auteurs.

Précis dans la lettre même, l'article 21 manque dans l'esprit d'une élasticité ou souplesse qu'il serait souhaitable d'y trouver quand surviennent certains cas de propriété d'auteurs non nécessairement exceptionnels.

Question de rafraîchir la mémoire d'un oubli toujours possible, voici en quels termes français on peut lire l'article 21: "L'auteur d'un nom scientifique est la personne qui la première a publié le nom en rapport avec une indication, une définition ou une description à moins qu'il ne soit évident par le contexte de la publication qu'une autre personne soit responsable du dit nom dans son indication, dans sa définition ou dans sa description."

Dans sa rédaction anglaise, l'article 21 se lit comme suit: "The author of a scientific name is that person who first publishes the name in connection with an indication, a definition, or a description, unless it is clear from the contents of the publication that some other person is responsible for said name and its indication, definition, or description."

Si l'on s'en tient à ces exigences, dans un esprit aussi rigide que le préconise la lettre de l'article, il nous faudra, en lieu de reviser plusieurs attributions de propriété scientifique, consacrer définitivement plusieurs erreurs de paternité scientifique que d'aucuns auteurs assignent tantôt à Provancher, tantôt à Huard, tantôt à Burque, à Brodie ou à Ashmead.

Tout en sachant parfaitement, par le texte de la publication, qu'une personne a partiellement ou entièrement contribué à la définition ou à la description d'une espèce nouvelle, il semble quelque peu inéquitable de lui en assigner la paternité d'auteur quand la publication de la définition ou de la description en est faite par une autre personne trois ou quatre ans après la mort de la première.

Il semble tout aussi inéquitable d'en accorder la propriété d'auteur au responsable de la publication quand sa seule participation fut d'en livrer la copie manuscrite à l'éditeur. L'article 21, tel que rédigé, laisse apparemment le choix à l'auteur d'attribuer la paternité à l'un ou à l'autre avec le résultat que certains auteurs l'assignent au descripteur apparent pendant que d'autres l'attribuent à l'éditeur.

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[1] A déja paru dans *Le Naturaliste Canadien* 84(1): 29-35. 1957.

Citons en exemple les quelque quarante espèces de névroptères, d'hémiptères et d'hyménoptères dont l'abbé Léon Provancher a préparé les descriptions peu de temps avant sa mort, survenue en 1892, et que certains auteurs assignent au Chanoine Victor Huart en se basant sur le fait que ce dernier en a assuré la publication en livrant les pages manuscrites au *Naturaliste Canadien* dont il a été l'éditeur-propriétaire de 1894 à 1929.

Notons de même certaines espèces dont le nom spécifique est *provancheri* et que plusieurs auteurs attribuent à Provancher lui-même. Ce n'est sûrement pas un tribut payé à la vertu d'humilité dont le révérend abbé n'a peut-être pas abusé dans ses écrits profanes mais qu'il pratiquait consciencieusement sur le plan scientifique.

C'est évidemment à tort que d'autres auteurs, encore tout récemment, accordent à Provancher la propriété entière d'*Echthrus provancheri* (Hymen.: Gelinae) dont la description originale apparait au *Canadian Entomologist*, 1885, vol. XVII, p. 116.

Et pourtant, on ne saurait non plus l'attribuer à Brodie sans rendre à ce dernier un hommage immérité. Bien que Brodie fut un assez fervent entomologiste amateur, il aurait été incapable, en 1885, de discerner les caractères d'une espèce nouvelle et d'en préparer une description scientifique en des termes appropriés.

Quelques mots d'explication supplémentaire aideront peut-être à mieux démontrer la cause d'erreurs qu'une trop stricte observance de l'article 21 peut occasionner.

Pendant les quelques années qui suivirent la publication de la première partie de la *Petite Faune Entomologique du Canada, en janvier 1874*, Provancher avait coutume de pratiquer, pour les entomologistes amateurs, de nombreuses identifications d'insectes de toutes sortes. Ceci naturellement, tant pour le spécialiste que pour l'amateur, présentait certains avantages. Pour l'un c'était d'avoir sous la main, dans un pays tout neuf et immense comme le nôtre, et sans qu'il en coûte beaucoup en frais de voyages assez difficiles dans le temps, une bonne quantité de matériel entomologique d'une faune encore inexplorée; pour l'autre c'était le montage d'une collection entomologique assez sûrement identifiée.

Or Brodie qui, en 1884, appliquait déjà depuis quelques années ce système peu onéreux et peu laborieux de se procurer une collection entomologique bien classifiée, voulut un jour faire preuve de gratitude envers Provancher et, dans cet élan de reconnaissance, le pria de lui permettre la dédicace d'une espèce nouvelle dont la publication serait faite en langue anglaise.

On sait pertinemment déjà que Brodie n'avait pas les connaissances suffisantes pour préparer la description scientifique d'une espèce nouvelle et que, s'il lisait assez bien le français et pouvait même le traduire quelque peu à l'occasion, il était tout aussi incapable de l'écrire que Provancher qui, de son côté, savait lire l'anglais et même le traduire suffisamment mais sans pouvoir l'écrire au point de préparer une description scientifique qu'exigeait sa probité professionnelle. Nous n'en voulons comme preuve que la volumineuse correspondance échangée entre lui et W.T. Harrington, d'Ottawa. Toujours en français de la part de Provancher, ou du moins presque, et toujours en anglais de la part de Harrington. Les quelques courtes lettres écrites en anglais par Provancher se terminent presque invariablement par la phrase: "Excuse my english, il est très mauvais."!

C'est pour cette raison d'ailleurs qu'il n'ose jamais répondre directement à Fletcher, d'Ottawa ou au Révérend Taylor de Vancouver. Il le fera par l'entremise de Harrington sans penser un seul instant que c'est là fausse honte de sa part car il a du moins l'avantage de comprendre l'anglais à la lecture ce que Fletcher et Taylor n'auraient su faire en français.

Les correspondances échangées tant de fois entre Provancher, Ashmead, Cresson, Coquillett, le Capitaine Gamble Geddes et Cockerell sont de même presque toujours en français de la part de Provancher et en anglais du côté des autres. Il faut excepter Coquillett qui parfois aimait écrire en français, ce qu'il faisait avec assez d'aise.

Pour en revenir à *Echthrus provancheri* voici comment les choses se sont passées. Dans un envoi assez considérable d'insectes que Brodie de Toronto expédie à Provancher en septembre 1884, il s'y trouve un certain nombre d'espèces que Provancher croit nouvelles à la science. Il en prépare donc immédiatement les descriptions françaises qu'il fait ensuite tenir à Brodie.

Ce dernier pratique rapidement la traduction, ou la fait pratiquer et, désirant toujours rendre hommage à Provancher, lui retourne le tout après avoir accolé le nom spécifique de *provancheri* au spécimen du genre *Echthrus* et en priant Provancher d'envoyer ces descriptions le plus tôt possible au *Canadian Entomologist* pour publication. "Please, dira-t-il dans sa lettre, send the enclosed descriptions to the *Canadian Entomologist* as soon as possible; you are better known than I am, it will certainly ensure the publication."

C'est donc dans ce groupe que l'on trouvera *Echthrus provancheri* (Hymen.: Gelinae) à la suite de quelle dénomination spécifique Provancher, précautionneusement d'ailleurs, ajoute le nom de Brodie en y joignant en plus une note explicative. Néanmoins, malgré ces précautions qui indiquent bien l'intention du signataire de l'article, presque tous les auteurs assignent la propriété de cette espèce à Provancher seul.

Les deux ayant presque également participé, l'un au texte même et l'autre à la traduction de la description, il semblerait plus dans l'ordre et plus dans l'esprit que devrait avoir l'article 21, d'en attribuer la paternité conjointement à Provancher et à Brodie plutôt qu'à Provancher seul ou à Brodie.

Les autres descriptions, y compris celle du nouveau genre *Platysoma*, publiées dans le même numéro du *Canadian Entomologist* et dans les mêmes conditions parce qu'elles faisaient part du même groupe devraient aussi être connues sous une paternité conjointe. Néanmoins le changement du genre *Platysoma* en celui d'*Aplomerus*, parce que le terme générique de *Platysoma* est déjà en usage, est bien de Provancher seul tel qu'il apparaît aux *Additions et Corrections de la Faune Entomologique du Canada*, 1886–1889, p. 119.

Ces mêmes erreurs se répètent encore, mais en sens inverse, dans le cas de *Callaspidia provancheri* (Hymen.: Figitidae) dont la description originale est publiée cette fois dans les *Additions et Corrections au volume 11 de la Faune Entomologique du Canada* traitant des Hyménoptères, 1885, p. 167 et que la plupart des auteurs, à la suite d'une note explicative de Provancher, attribuent cette fois à Ashmead. Ce geste de la part des auteurs est complètement en contradiction avec ce qu'ils pratiquent dans le cas de Brodie.

Dimicrostrophis ruficornis (Hymen.: Cynipidae) dont les descriptions générique et spécifique apparaissent aux pages 172 et 173 du même volume, avec une autre note explicative à peu près identique à la précédente, est encore un exemple de propriété conjointe nonobstant que les auteurs en général assignent et le genre et l'espèce à Ashmead seul.

Les espèces *Lyda provancheri et Lyda chicoutimiensis* (Hymen.: Pamphiliidae) dont les descriptions sont publiées au *Naturaliste Canadien*, vol. XI, 1879, p. 148–149, première pagination, sont aussi dans le même cas d'erreur malgré la signature apparente de l'abbé V. Huart. Le contexte de l'article sous le titre: "Une nouvelle espèce de *Lyda*" et qui nous amène aux deux descriptions ne prête nullement à équivoque et démontre bien que Provancher est conjointement l'auteur tant de l'article que des descriptions.

Quant à *Trogus provancheri* (Hymen.: Ichneumonidae) assigné à l'abbé Burque de St-Hyacinthe, contrairement à la première impression que laisse l'article qui précède les descriptions, il n'y a pas lieu de s'y laisser prendre. La correspondance échangée entre Burque et Provancher à ce sujet et dont des extraits sont publiés en même temps nous indique clairement que Provancher est, tout au moins pour la majeure partie, l'auteur de l'article et de la description tout comme de l'indication du rang que l'espèce occupe dans la clef analytique abrégée qui suit la description.

Il serait possible de citer encore de nombreux cas à peu près identiques mais nous croyons que les exemples précédents suffisent à démontrer ce que nous voulions établir, à savoir: Que l'article 21 du Code international de Nomenclature zoologique manque quelque peu de souplesse dans son application de paternité scientifique.

En conclusion, à la lumière des constatations qui précèdent, il est de notre intention, au Musée de la province de Québec, à titre de dépositaires des trois grandes collections entomologiques de Provancher, de publier bientôt une révision complète des quelque quinze cents types décrits par Provancher et certains de ses collaborateurs.

En ce faisant, nous respecterons, autant que faire se peut, la lettre de l'article 21 du Code international mais en lui accordant la souplesse d'interprétation nécessaire. Nous formulons le voeu que les auteurs, subséquemment à la publication de cette révision, feront de même, rendant à César ce qui appartient à César et à Provancher ce qui appartient à Provancher.

Distributional and Nomenclatorial Problems in Some Forms of *Vespula* in North America (Hymenoptera: Vespidae)[1]

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ABSTRACT

New and old taxonomic characters used to define some entities in the genus Vespula *are examined and correlated with distributional information. The results strongly indicate that the present nomenclatorial interpretation of certain forms does not portray correctly the way they perform in nature and vividly show that a study of museum specimens alone is insufficient to understand the taxonomy of the group. A short discussion indicates the additional work needed to produce the information necessary to understand the character of the forms involved.*

Most systematists are aware that speciation is not always accompanied by structural change and that structural change does not always indicate that a species has evolved, yet most workers continue to accept Bequaert's classification of the North American species of *Vespula* (Bequaert, 1931), which was based on his belief that biological forms should afford structural differences before they should be ranked as species.

The following are facts concerning some of these forms. After examining them I think one will agree that Bequaert's nomenclatorial interpretation of the forms involved does not correctly portray the manner with which they perform in nature.

Let us examine the facts concerning the North American forms of *Vespula* presently treated in the literature as color varieties or subspecies of *Vespula rufa* (Linne). Except for one, these forms are, as recorded by Bequaert, structurally similar to the European species. Fig. 1 illustrates the abdominal color patterns of the male, female and neuter of two forms currently called *V. rufa* var. *consobrina* (Saussure) and *V. rufa* var. *intermedia* (Buysson). They are both black and white forms. *Intermedia* has rufous markings on the first and second tergites and sternites, as indicated in the figure by stipling. These patterns are typical for each form and exceedingly stable over each of their ranges (Figs. 4, 5). No specimens of these forms have ever been found with intergradient color patterns. Further, the few nest series of *consobrina* that I have been able to examine have shown insignificant variation.

Illustrated in Fig. 2 is the abdominal color pattern of the male, female and neuter of the forms treated by Bequaert as *V. rufa* var. *atropilosa* (Sladen), *V. rufa* var. *sladeni* Bequaert, *V. rufa* var. *acadica* (Sladen) and *V. rufa* var. *vidua* (Saussure). These forms are black and yellow. It is important to explain here why Bequaert proposed this nomenclatorial interpretation for these forms. The following is an account of the circumstances which lead him to his decision.

During the course of his study on the genus. Bequaert obtained an occasional male and neuter specimen which had an abdominal color pattern intermediate between *atropilosa* and *sladeni* from the area where their ranges overlapped. He also obtained an occasional male and neuter specimen which had an abdominal color pattern intermediate between *vidua* and *acadica* from the area where their ranges overlapped. Further he noted that the forms *acadica* and *sladeni* were identical. In addition the distributional data he had available placed the ranges of *acadica* and *sladeni* in the east and western regions of North America respectively. Although he knew that Sladen (Sladen, 1918) had described the form as one species, there was still no evidence that its range was continuous from coast to coast, there was a tremendous gap in the central region of North America where no specimens of *acadica* or *sladeni* had ever been found. Taking these facts into consideration, realizing the close structural relationship of all these forms and knowing the distribution of *vidua* and *atropilosa* (Fig. 6) he proposed the following theory. He claimed that through evolutionary convergence *atropilosa* and *vidua* each produced a northern race, or subspecies which were similar, (so similar that it is impossible to tell them apart). Though he realized this similarity he believed two entities were involved, hence the names *V. rufa* var. *acadica* and *V. rufa* var. *sladeni* were used for this single form. I say single form because

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[1] Contribution No. 3607, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

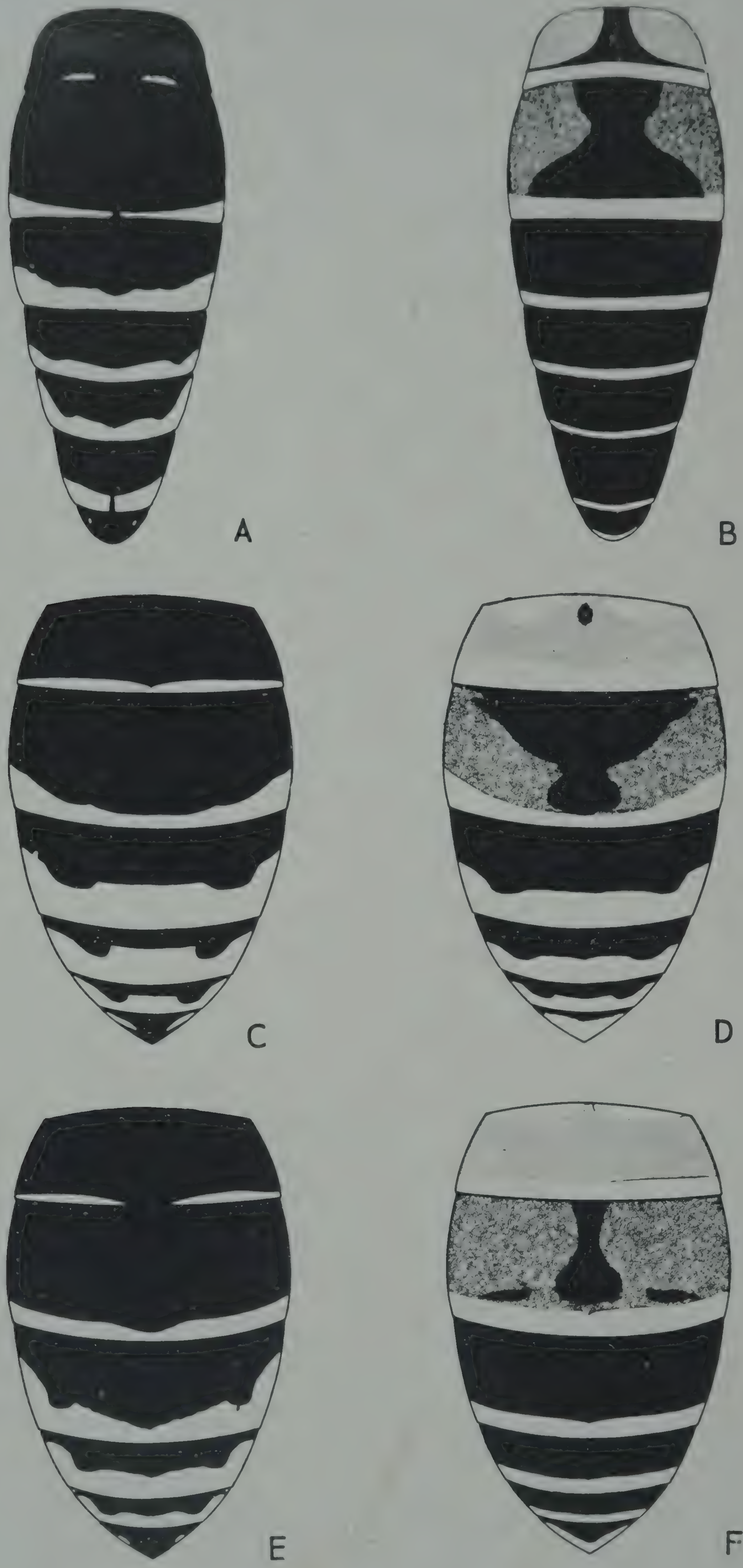
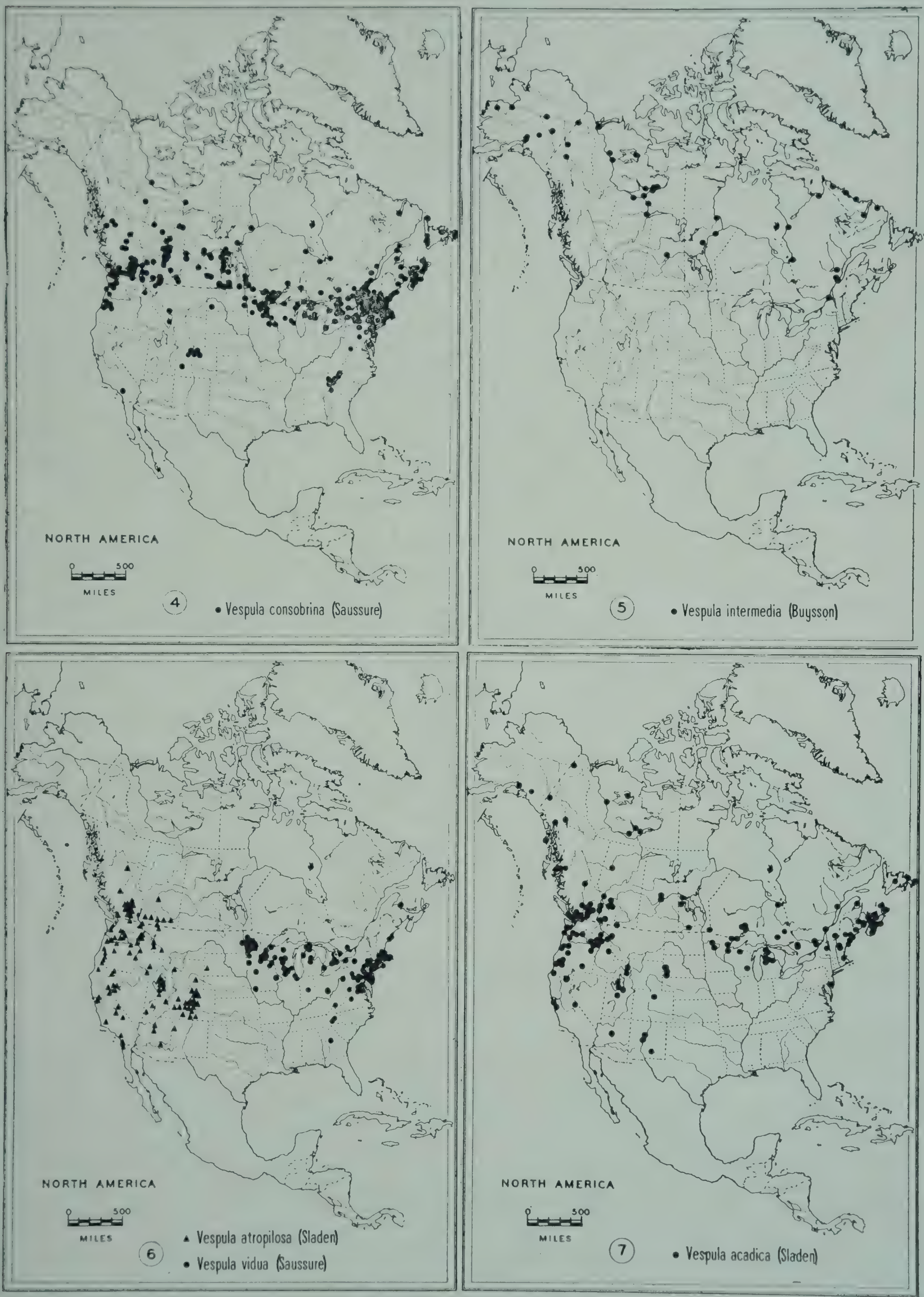


Fig. 1. Typical abdominal color patterns of *Vespula* spp. A, male; C. female; E, neuter of *consobrina* (Saussure) [=*rufa* var. *consobrina* (Saussure)]. B, male; D, female; F, neuter of *intermedia* (Buysson) [=*rufa* var. *intermedia* (Buysson)].

they are identical in appearance and as one can see in Fig. 7 its range is continuous from coast to coast. In addition I have recently found that *vidua* is structurally different from *rufa*, *acadica*, *atropilosa*, *consobrina* and *intermedia*. The difference is apparent when one compares the male genitalia of *vidua* with that of any one of the other forms. The male genitalia of *rufa* and *vidua* are illustrated in Fig. 8. As one can see, the comparative length of the digitus and distal saddle-shaped portion of the aedeagus is significantly different in each form. In addition, the pilosity of the abdominal tergites of *vidua* is short, sparse and obscure, while that of *rufa acadica*, *atropilosa*, *consobrina* and *intermedia* is long, numerous and well defined.


NORTH AMERICA
0 500
MILES
4
• Vespula consobrina (Saussure)
NORTH AMERICA
0 500
MILES
5
• Vespula intermedia (Buysson)
NORTH AMERICA
0 500
MILES
6
▲ Vespula atropilosa (Sladen)
• Vespula vidua (Saussure)
NORTH AMERICA
0 500
MILES
7
• Vespula acadica (Sladen)

Figs. 4–7. Distributional patterns of *Vespula* spp. 4, *consobrina* (Saussure). 5, *intermedia* (Saussure). 6, *atropilosa* (Sladen) and *vidua* (Saussure). 7, *acadica* (Sladen).

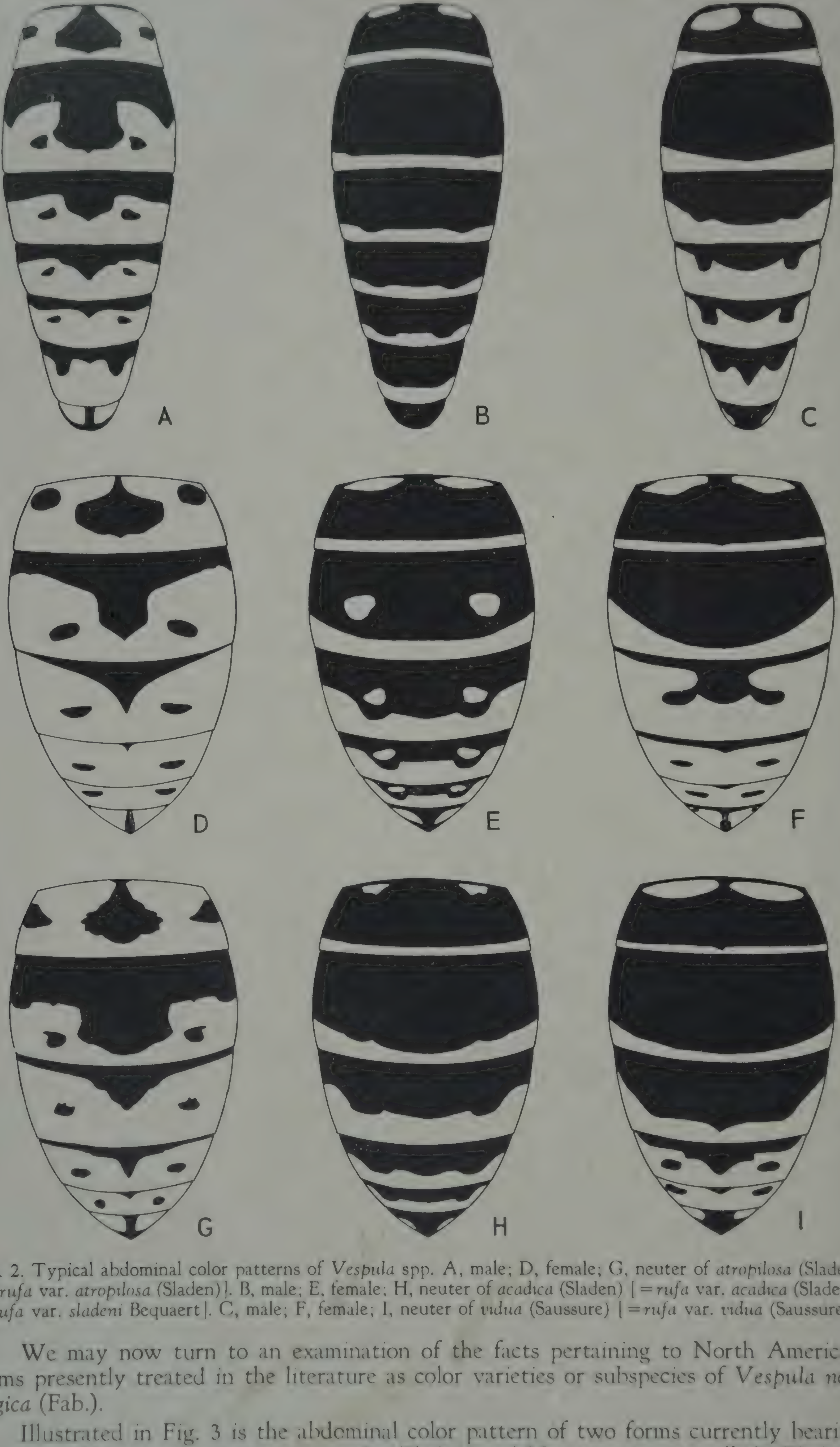


Fig. 2. Typical abdominal color patterns of *Vespula* spp. A, male; D, female; G, neuter of *atropilosa* (Sladen) [=*rufa* var. *atropilosa* (Sladen)]. B, male; E, female; H, neuter of *acadica* (Sladen) [=*rufa* var. *acadica* (Sladen), =*rufa* var. *sladeni* Bequaert]. C, male; F, female; I, neuter of *vidua* (Saussure) [=*rufa* var. *vidua* (Saussure)].

We may now turn to an examination of the facts pertaining to North American forms presently treated in the literature as color varieties or subspecies of *Vespula norwegica* (Fab.).

Illustrated in Fig. 3 is the abdominal color pattern of two forms currently bearing the names *V. norwegica* var. *norvegicoides* (Sladen) and *V. norwegica* var. *albida* (Sladen).

Albida is black and white. Usually, rufous markings are present on the first and second abdominal tergites and sternites of the males and neuters, but they have never been noted in the female. *Norvegicoides* is black and yellow and has no rufous markings. The distribution of the form *albida* is shown in Fig. 9 and that of *norvegicoides* in Fig. 10.

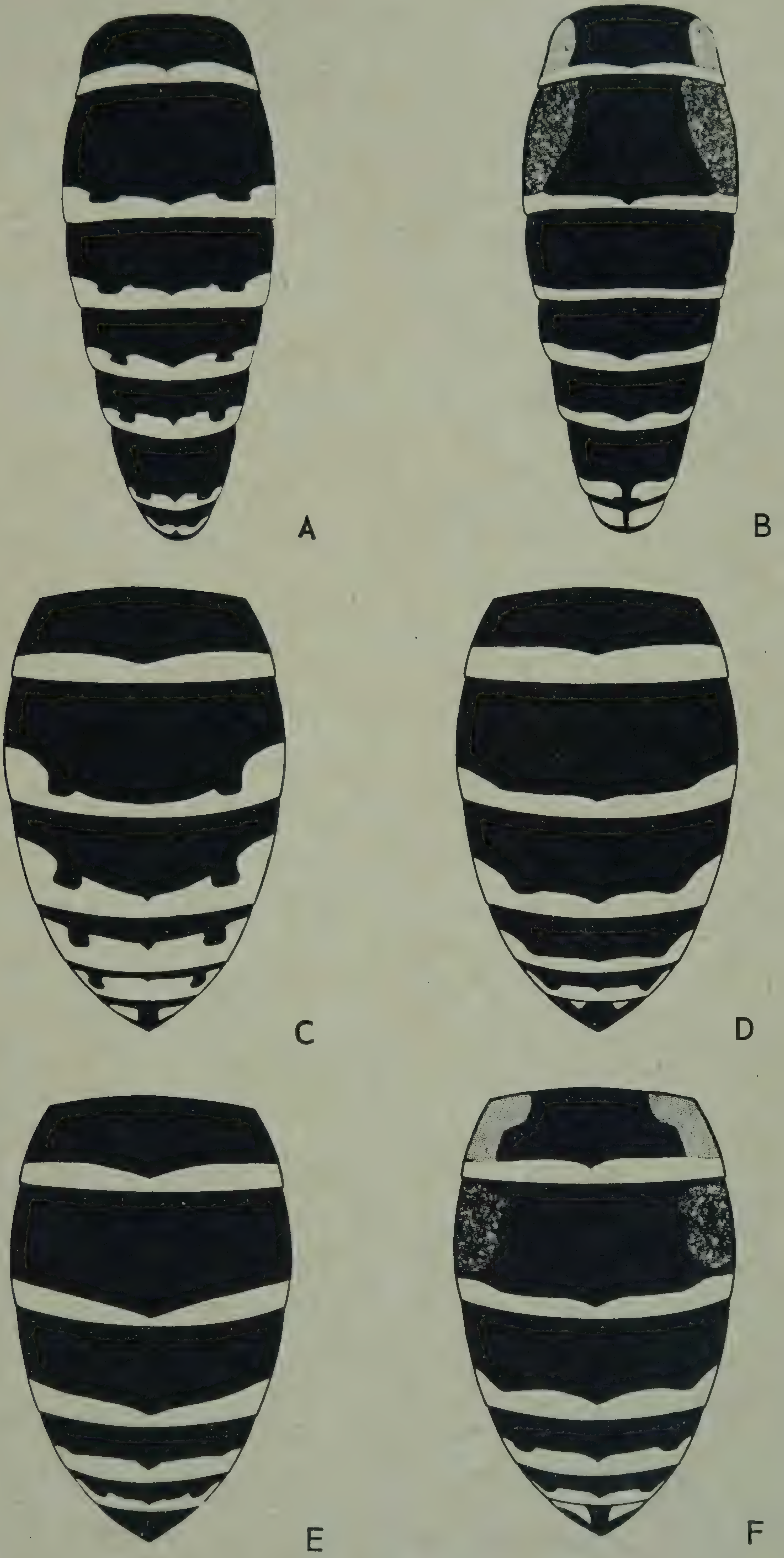
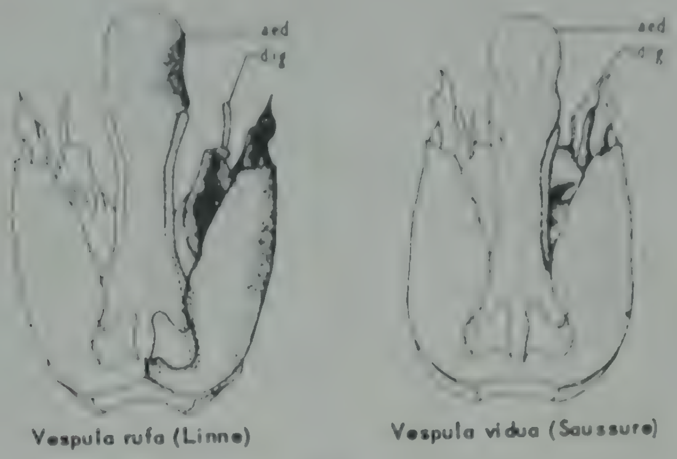


Fig. 3. Typical abdominal color patterns of *Vespula* spp. A, male; C, female; E, neuter of *norvegicoides* (Sladen) [=*norwegica* var. *norvegicoides* (Sladen)]. B, male; D, female; F, neuter of *albida* (Sladen) [=*norwegica* var. *albida* (Sladen)].



8

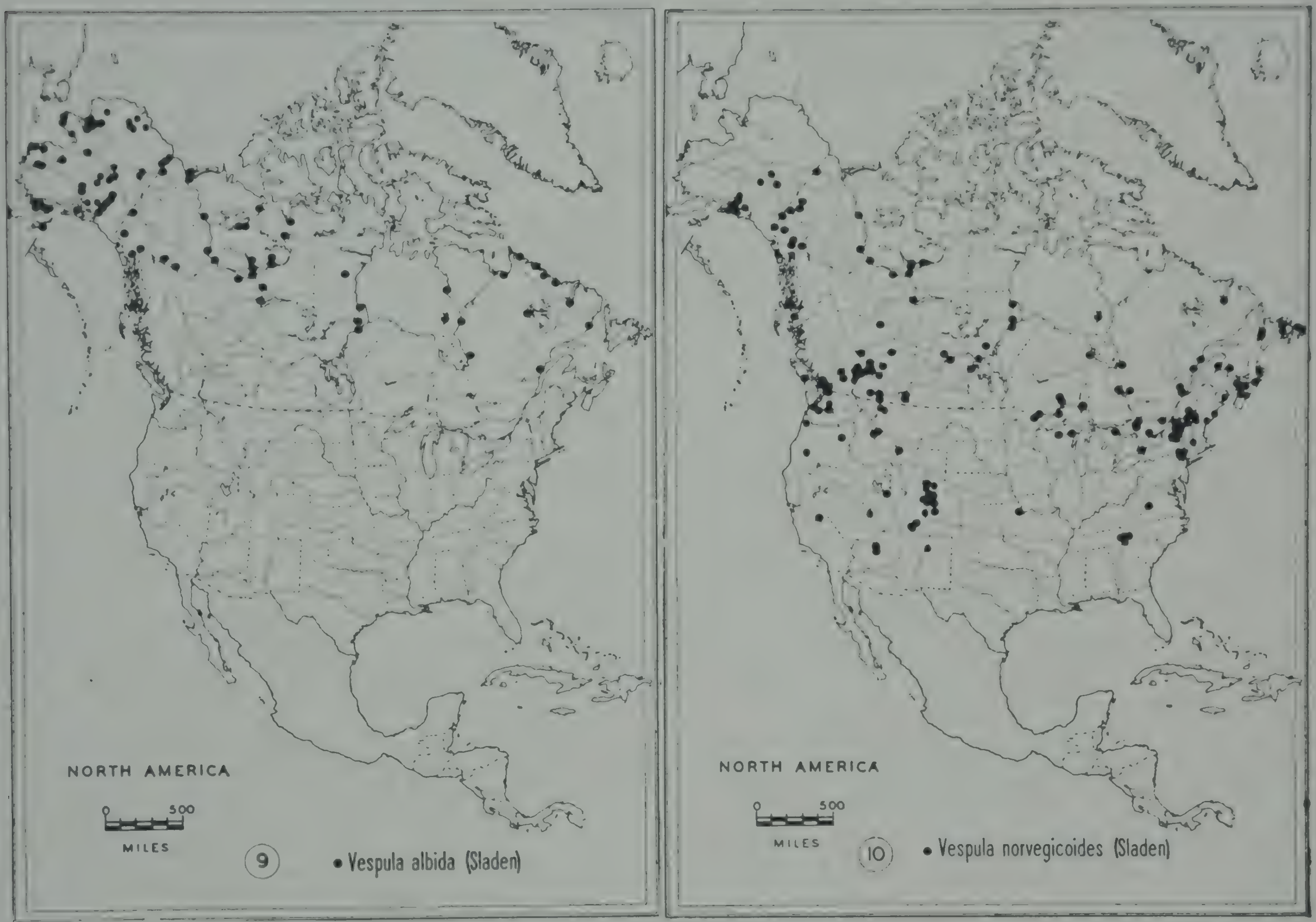


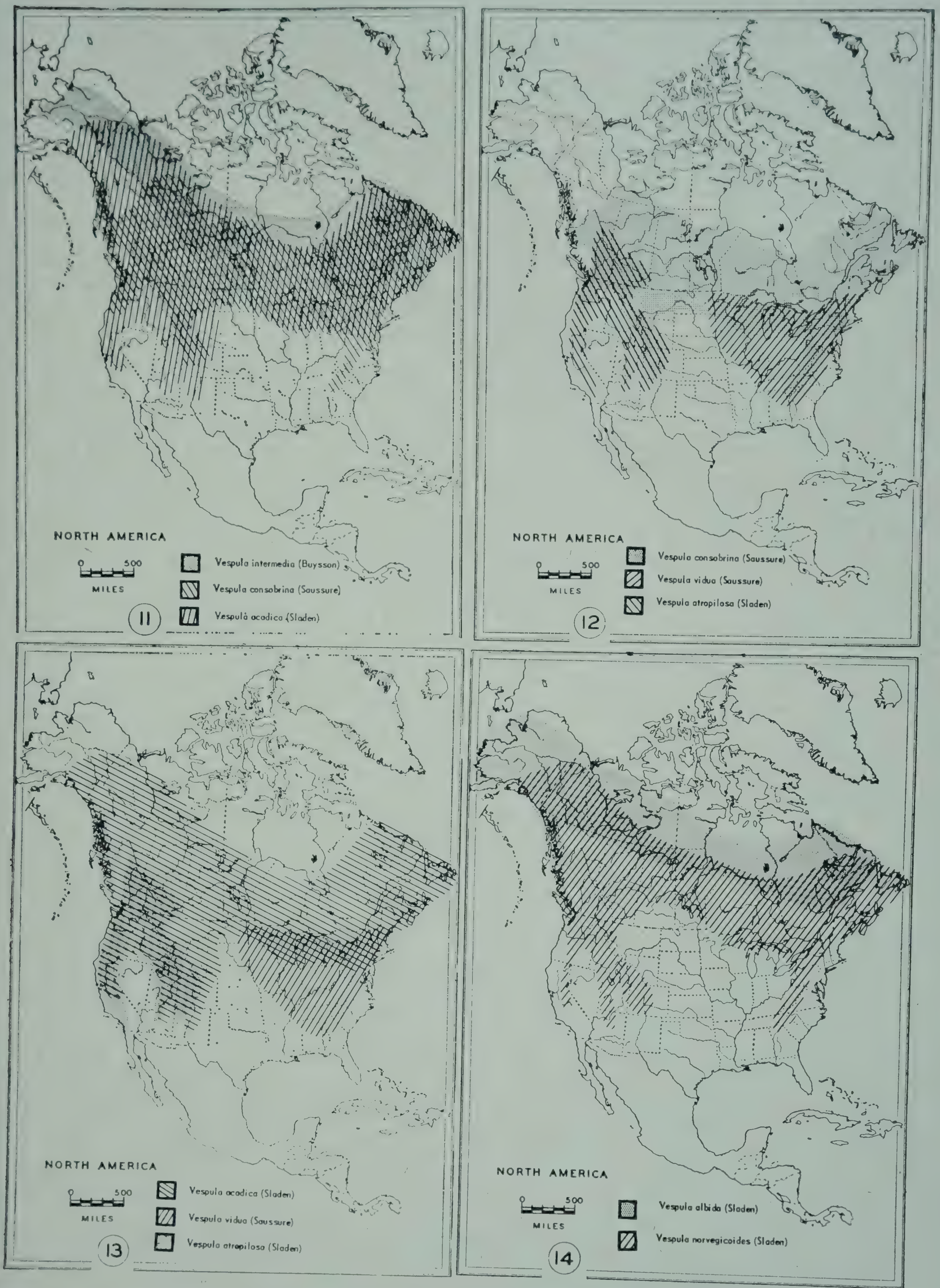
Fig. 8. Dorsal aspect of the male genitalia of *Vespula rufa* (Linne) and *vidua* (Saussure) [=*rufa* var. *vidua* (Saussure)]. aed, aedeagus; dig, digitus.

Figs. 9, 10. Distributional patterns of *Vespula* spp. 9, *albida* (Sladen). 10, *norvegicoides* (Sladen).

Bequaert's treatment of these two forms appears to be somewhat contradictory, in that in his general remarks on the genus he states that "Only such forms are given specific rank as are separable by means of reliable structural peculiarities in at least one of the sexes", whereas in his key to the males he indicates that the last five segments of the flagellum of the male of *albida* have a single tyloid near the base, and that the last six segments of the flagellum of *norvegicoides* have two tyloids, one near the base and one near the apex. Yet he treats them as color varieties or subspecies. No specimens of these two forms have been found which have intergradient color patterns.

We may now examine all the above facts in a comparative manner. The distribution of *intermedia*, *consobrina* and *acadica* are shown in Fig. 11. As may be seen their ranges are partially or almost entirely sympatric. Structurally the forms are identical, but each has a distinct color pattern which is constant throughout its range. No intergradient patterns have been found.

The distributions of *consobrina*, *vidua* and *atropilosa* are shown in Fig. 12. It will be noted that their ranges widely overlap. *Consobrina* and *atropilosa* are structurally similar, but *vidua* is distinct. Each has a distinct color pattern which is constant throughout its range. No intergradient patterns have been found.


NORTH AMERICA
0 500
MILES
Vespula intermedia (Buysson)
Vespula consobrina (Saussure)
Vespulà acadica (Sladen)
11
NORTH AMERICA
0 500
MILES
Vespula consobrina (Saussure)
Vespula vidua (Saussure)
Vespula atropilosa (Sladen)
12
NORTH AMERICA
0 500
MILES
Vespula acadica (Sladen)
Vespula vidua (Saussure)
Vespula atropilosa (Sladen)
13
NORTH AMERICA
0 500
MILES
Vespula albida (Sladen)
Vespula norvegicoides (Sladen)
14

Figs. 11–14. Distributional patterns of *Vespula* spp. 11, *intermedia* (Buysson), *consobrina* (Saussure) and *acadica* (Sladen). 12, *consobrina* (Saussure), *vidua* (Saussure) and *atropilosa* (Sladen). 13, *acadica* (Sladen), *vidua* (Saussure) and *atropilosa* (Sladen). 14, *albida* (Salden) and *norvegicoides* (Sladen).

The distribution of *acadica*, *vidua* and *atropilosa* are shown in Fig. 13. Their ranges widely overlap as well. *Atropilosa* and *acadica* are structurally similar, but *vidua* is distinct. The color pattern of the female is always distinct, but occasionally a male or neuter specimen occurs which has an abdominal color pattern intergradient between *acadica* and *atropilosa* or between *acadica* and *vidua* from the areas where their ranges overlap.

The distribution of *albida* and *norvegicoides* are shown in Fig. 14. Their ranges are partially sympatric. They have distinct color patterns and the males are structurally separable.

Now, knowing the facts concerning these entities, is it possible to believe that they interbreed freely and still maintain their identities over their ranges, even when these are partially or almost entirely sympatric? I think the above evidence strongly indicates that they do not interbreed freely in nature but are definitely isolated by some unknown mechanism.

In closing I would like to point out that I am well aware that the facts given in this paper do not solve the problems involved in the classification of the genus *Vespula*, but merely elucidate them. Except for a statistical analysis of relative sizes of the forms involved, I believe I have gone as far as anyone can go with the study of museum specimens. Further evidence concerning the manner with which these entities perform in nature will have to come from field studies and study of live material. Nests will have to be found. This is not an easy task. The habits and life histories of the tenants will have to be recorded and pertinent biological differences determined.

Live material should be supplied to geneticists and physiologists to allow them an opportunity to study chromosone patterns, run chromatographic and precipitin tests.

When all this is done then one can point to a specimen of *Vespula* and without any doubt say, this is the species *Vespula consobrina* (Saussure), because every available measuring stick has been used to determine its zoological status.

REFERENCES

Bequaert, J. 1931. A tentative synopsis of the hornets and yellow-jackets (Vespinae; Hymenoptera) of America. *Entomologica Americana* 12: 71–138.

Sladen, F. W. L. 1918. The genus *Vespa* in Canada. *Ottawa Naturalist* 22: 71–72.

DISCUSSION

H. TOWNES. Now that the speaker has questioned the traditional treatment of specific and subspecific names in *Vespula*, it may be in order also to question the generic name. It seems to me that Bequaert overemphasized the importance of the shape of the temple in separating *Vespula* and *Vespa* and that perhaps a more natural arrangement would unite *Vespula* and *Vespa* and would separate *Dolichovespula* as a distinct genus, as did Schmiedeknecht.

C. D. F. MILLER. I have not studied the generic concepts so am not prepared to answer the question.

The Phylogeny of the Hymenoptera

By J. Chester Bradley
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ABSTRACT

The Hymenoptera arose from a common stem with the holometabolous orders Lepidoptera and Trichoptera in the Jurassic period. Larval food-habits and provision made for the larvae by the adults have been the significant features of their evolution. The early Hymenoptera were Chalastogastra, with leaf-eating larvae, direct competitors of caterpillars, which they resembled. A revolution in food-habits produced the higher suborder, Clistogastra. The larvae became parasites, chiefly on the holometabolous orders or Homoptera. This was a new method of living not previously exploited by other insects. It was the cause of the prodigious evolutionary success of the suborder. Substitution of the plant host for an animal has occurred several times. In the Aculeata, a second evolutionary line of Clistogastra, further development of the poison gland, transformation of the ovipositor to a sting, and ability of the poison to keep the host larva alive but comatose has led to the development of a domicile and sense of property right. Steps could thereafter lead to the complex gynarchic societies of the ants, bees, and wasps, the summit of invertebrate evolution. Pollen and honey became the final larval food.

The mayflies, dragonflies, and certain extinct orders form the more primitive evolutionary division of winged insects termed Paleoptilota. The other winged insects, Neoptilota, although also dating back to the Carboniferous, are further evolved. They have developed along three or four lines which we may regard as superorders. The most advanced and the most clearly defined of these is the superorder Holometabola, a significant feature of which is the transformation of the early nymphal stages into a specialized creature which we call larva, capable of sustaining a life at complete variance with that of the adult. This specialization, coupled with the eventually quiescent stage during which the individual is being made over, the pupa, has given them an advantage over all other insects. It is only among them that the numerically enormous, preeminently successful orders have developed.

The Hymenoptera is one of four such orders. Reaching, by reason of its social organization, the summit of invertebrate evolution, it had its beginnings in forms no more evolved than the earliest Lepidoptera or Trichoptera. Two facts have interfered with an understanding of the origin of Hymenoptera. First: the venation-pattern was misinterpreted by Comstock, and as a result resisted attempts to relate it closely with other orders; secondly: the great number of malpighian tubes in many Hymenoptera has misled some students. We now know that the venation is not overly complex. The anal region is closely similar to that of the Jugatae, of the Trichoptera, and of the Mecoptera, and the interpretation of the hind wing reveals the interpretation of the more complete venation of the forewing. The primitive number of malpighian tubes in insects seems to have been six. But this number has been both increased and decreased repeatedly in the course of evolution. One of the tendencies within the order Hymenoptera has been toward increase in the number of these tubes, but in some primitive forms the number is still comparatively few.

The resemblance between the larvae of sawflies, of primitive Trichoptera, and of caterpillars is not, as sometimes thought, a coincidence of convergence, but is a result of close relationship resulting from a common ancestral stem.

The Hymenoptera arose in the Jurassic period, probably in the Northern Hemisphere, among the extensive coniferous forests of that period. The very primitive subfamily Siricinae is still confined to coniferous trees.

The key to the evolution of Hymenoptera has been the food habits of the larvae and the provision made for them by the adults. As larvae, the early Hymenoptera were leaf-eaters and borers and therefore direct competitors of lepidopterous caterpillars. They had acquired no new bionomic feature to give them an advantage. They were the suborder Chalastogastra, as we now divide Hymenoptera, and would have remained an insignificant order had not a new and startling development given rise to a higher suborder with almost limitless bionomic possibilities. That new development was parasitism on the part of the larvae.

How parasitism arose is problematical. The first step must have been the substitution of animal food in place of vegetable food. This appears not to have been, physiologically, a fundamental difference, for we find a reversion to plant food occurring later several times in the course of the onward evolution of Clistogastra. Prior to parasitism there must have been a stage when the larvae, in process of adopting an animal diet, ate indifferently plant material or other insect larvae which they chanced to encounter. Gradually a dependence upon the latter must have arisen. The food supply of leaf-eaters, within season, is unlimited; but sufficient supply for flesh-eaters is fortuitous. Carnivorous larvae that lived in a confined situation, such as in a boring, unless they could wander from burrow to burrow, must have lived upon the borer without killing it until such time as their own nutritional needs were terminating, at which time they could gorge themselves in a final feast and discard the host. That is exactly how the larvae of parasitic Hymenoptera do conserve their limited food supply until their growth is attained.

So parasitism came about and with it the evolution from the suborder Chalastogastra to the suborder Clistogastra. The structural changes that accompanied this bionomic step were perhaps as great as those which usually distinguish orders of insects rather than suborders. The larvae became quiescent, maggot-like, and lost both abdominal and thoracic legs. The change of ovipositor from a saw-like type to a piercing egg-laying tube was correlated with new necessities in egg-laying. But methods of egg-laying employed by the parasitic Hymenoptera required a flexibility of the abdomen not useful to sawflies. Such flexibility was attained by the development of a constriction and highly flexible joint between the first and second abdominal segments, leaving the first of these segments fused to the metathorax, as part of the alitrunk, while the balance of the abdomen became a mobile division of the body that simulates a complete abdomen.

Between these two suborders lies the annectent family Oryssidae. Their body-structure is like that of other Chalastogastra, but the ovipositor is like that of some Ichneumonoidea, a long flexible tube like a hypodermic needle, which indeed may be retracted into and coiled within the abdomen. Oryssidae are parasites of wood-boring Coleoptera. They have acquired the habits of Clistogastra, but except for the ovipositor, not the structural adjustments. The late S. A. Rohwer proposed for them a third suborder, but on balance they may better be left in the Chalastogastra where they form, as just demonstrated, an evolutionary link with the Clistogastra, although certainly not as direct ancestors.

When the larvae of Hymenoptera became parasites, undergoing corresponding degenerative changes, and the adults acquired new characteristics to meet changed necessities of egg-laying, they initiated a new manner of life that had not previously been exploited by insects or by other animals. Following Wheeler, we may call them parasitoids, because only the larvae are degenerate and parasitic. Eventually they were to meet competition from the dipterous family Tachinidae, but at the start they had the field to themselves and made the most of it. It was the key to their success and enormous numbers.

For the most part these Clistogastra parasitize insects of the holometabolous orders or Homoptera, great orders with which their development kept pace. It is interesting to note that while a few have parasitized spiders none have parasitized apterygote insects and very few attack insects of the lower orders, and these few are almost exclusively egg-parasites.

Within the Clistogastra the family most closely related to the Chalastogastra is the Braconidae. This is proven by the fact that in diverse genera scattered through various sections of the family stumps of one or another of the veins of the anal region of the forewing have been retained. These are remnants of the anal veins that occur in Chalastogastra but not in other Clistogastra. The Braconidae evolved before loss of these veins became complete. It is conceivable that some other primitive families of Clistogastra could have at first retained these veins and subsequently lost them, but we have no evidence to that effect. Neither am I aware of structures characteristic of the Chalastogastra that have been retained in other families of Clistogastra but lost in the Braconidae, except the posterior lobe of the hind wing, and, in some aculeates, a spur of the usually-lost base of the first radial cross-vein.

The superfamilies[1] Ichneumonoidea, Prototrupoidea, Cynipoidea, Chalcidoidea, and Evanioidea form one evolutionary line of the Clistogastra, the parasitoid Hymenoptera, the remaining superfamilies form the second line, the aculeata.

The parasitoid line, as just demonstrated, was initiated with the Braconidae. The larvae live a quiescent life. Those that are internal parasites are bathed in a nutrient fluid which they absorb. There is no problem of food supply as long as the host remains healthy. Therefore they have to avoid eating anything that will terminate the life of the host and thereby their own food supply until they are full-grown and no longer need it. Then they usually consume the remainder of the body contents of their host in a final glutinous feast. The more specialized forms have completely synchronized their development with the relevant steps of their host's life-history, and frequently pass over from one stage of the host into another.

Two or more times in the Chalcidoidea and independently in the subfamily Cynipinae of the Cynipoidea plant-tissue has been substituted for animal tissue on part of the host. But there has been no fundamental change in the manner of life. The larvae still live a quiescent life, bathed by nutrient fluid. The gall-producing habits of the Cynipinae form a side-wise ethological specialization of great interest, but without significance in the onward evolution of the order.

Atrophy of the wing-veins to the point of almost complete loss of their pattern has occurred independently in Proctotrypoidea, Chalcidoidea, and Evanioidea. In understanding the relation of these superfamilies, the venation gives the clearest evidence. Following the Ichneumonoidea, the Proctotrupoidea must come first, having retained in its lower families a complete venation. It must be followed by 1: Cynipoidea and 2: Chalcidoidea. As I have shown in a recent article[2], the wing-venation of the latter can only be derived and interpreted from that of the former, *Ibalia* and *Leucospis* being the annectent forms.

At least some primitive members of all families of aculeate Hymenoptera, in common with Chalastogastra and other orders, possess a posterior lobe of the hind wings. This is retained by no parasitoids except the abberrant family Evaniidae. It clearly was lost, once and for all, early on the parasitoid stem, but *after* the separation of that stem from the aculeates[3]. The Evaniidae, which possess this lobe, are so different from all other parasitoids that it is best to allocate them as a special superfamily at the base of the two main stems. It may not be without significance that they all parasitize eggs of cockroaches, which were abundantly available when the first Clistogastra were developing.

Success in life for a parasitoid depends upon successful completion of the growth of its host larva, or of whatever stage it parasitizes. The hosts are not given any special protection, hence suffer all the vicissitudes of an exposed life. The next evolutionary step, marking the aculeate stem, changed this state of affairs. The poison-glands, already present as an appendage of the ovipositor, were specially developed, emptying through the ovipositor. The latter no longer served for egg-laying, but has became a short aculeus or sting, serving as a hypodermic needle for injection of poison.

In such a very primitive aculeate as *Scolia* the poison from the sting tends to feebly paralyze the host larva, and a very crude cell is worked out around the latter in the earth. In more advanced forms the paralysis becomes complete and a perfect nest is formed. This paralyzed condition may be likened to cold storage. The host is kept alive but comatose, hence fresh and edible, until the parasitic larva is grown. At the same time both parasite and host are protected from the vicissitudes of an open, free-living existence by the artifice of a nest.

Here we have the beginning of property-right and a domicile, phenomena rare among invertebrates. The domicile is at first only for the larvae, but in later development is shared by the mother, or even an entire family. The sense of ownership is so imbued in these insects that in higher social forms any invasion or intrusion into the nest is vigorously repelled by the entire household.

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[1] The superfamily names apply as used in the phylogenetic classification of Hymenoptera devised by Bequaert, Rohwer, Maidl and Bradley and published in Comstock's Introduction to Entomology, 1924.

[2] The wing-venation of Chalcidoidea and of some allied Hymenoptera. *Mémoires de la Société Royale d'Entomologie de Belgique*, volume jubilaire, 1955 [July, 1956], p. 127–138, incl. pl. I–V.

[3] The aculeate stem must be regarded as diverging from the parasite line at the very base of the suborder Clistogastra, probably before the clear differentiation of any of the groups now known to us.

In the recent catalog of North American Hymenoptera the aculeates have been divided into six superfamilies. These represent natural groups of unequal value, possible somewhat arbitrarily chosen. The difficulties of deciding where to limit these superfamilies is considerable. I am not aware that any one has successfully differentiated all of them either morphologically or on the basis of bionomics. There are, however, two major lines of development, marked by a certain difference of thoracic structure, and I suggest that it may most nearly represent the evolutionary development to recognize each of these two and only these as superfamilies, namely *Vespoidea* and *Sphecoidea.* Of these the *Vespoidea* contain the more primitive types, and are more diverse. They should be placed first.

When property is accumulated and labor expended, there are always those who seek to get a free ride through life by living within the property of the others, or at the expense of their labors. The Hymenoptera are no exception. Social parasites have arisen time and again in numerous families. I use the term somewhat more broadly than Wheeler or Roubaud, to indicate all cases where the parasitic species lives at the expense of the property or labors of the host, rather than merely on its body. Ceropales is a well-known example. It enters the nest of Pompilus and lays its eggs in the book-lungs of the spider with which the female Pompilus has provisioned its nest for the use of its own offspring. Other examples are the many cuckoo-genera of wasps and of bees. More complex are the social parasites in the restricted sense, as the term is used by Wheeler. These are descendants of species that, in the past, have maintained fully developed societies such as characterize the social wasps, ants, and bees, but by a process of degenerative evolution have now become dependant upon allied species or genera to initiate and usually to maintain their colonies. Thus *Bothriomyrmex decapitans* takes over a colony initiated by *Tapinoma*; certain species of *Vespa* can only maintain their families in the nests of other kinds of *Vespa* and the species of *Psithyrus* only in the nests of certain species of bumble-bees.

The fascinatingly interesting steps which have led to the development of social aculeates independently among the ants, Vespidae and bees have been so thoroughly described by Wheeler[4] that they need no repetition here, but should be born in mind; for these groups represent the evolutionary summit of each of three lines of aculeates. Together, with termites, they represent the highest evolution attained among the invertebrates, where their position may be compared to that of man within the Vertebrata.

Some Vespidae (*Masarinae*) feed their larvae on pollen and honey and some store honey, for example *Brachygastra*, formerly called *Nectarina*. This represents a final revolution in larval food-habits, and is a return to plant-food, but of a vastly more refined type than the crass leaf-chewing habits of sawfly-larvae.

The pollen-and-honey-feeding habit has been independently acquired by bees, which are to sphecoid wasps what Masarinae are to Vespidae. All of the structures that distinguish bees are adaptive modifications for collecting pollen. Bees that are social parasites of other bees, have again lost such adaptations. No one has pointed out a satisfactory morphological character for separating all bees from Sphecidae. The bees have been an extraordinarily successful group and have become very numerous. On this account some hymenopterists deem it convenient to constitute them a special superfamily. However, to do so would seem to throw a phylogenetic classification somewhat out of balance, by overemphasizing the difference between them and Sphecidae.

We have seen that the purpose which the sting served, when first developed, was to render the food of the larva comatose, and thus to preserve it during the growing period of the latter. Some wasps, such as the Bembicinae, feed their young with fresh animal food each day. As a result the sting has lost its importance. In those Hymenoptera that provision their larvae with pollen and honey, nothing of the original function of the sting remains, but in the social species, it has assumed a new use, being called upon for colonial defense in repelling any intruder. Finally, following its lessened importance, the sting has entirely disappeared in many ants and in the stingless honey-bee. These resort for defense of the colony to the effect that multitudes of individuals can perpetrate by biting, tweaking, or discharging irritating anal fluids. It is a little difficult to see why such methods of defense have supplanted stinging or to look upon them as an improvement.

Such has been the comparatively swift evolution of the order. Beginning in the Jurassic as leaf-eating or wood-boring caterpillars with moth-like but scaleless adults, they became parasitoids of free-living insects, without disturbing the normal life of the latter. Then, with development of the sting, they became builders of homes which they provision with preserved animal food. Afterwards such food was abandoned in favor of honey and pollen, or sometimes other agricultural products such as seeds or fungi. Side-lines have repeatedly developed into social parasites, dependent upon the domiciles and labor of their aculeate hosts. Finally several times independently great gynarchic societies have arisen in which the welfare of the colony is all-important, the fate of the individual of no significance, a social organization, which, in the words of the late Dr. Wheeler, is so utterly incommensurate with our own society, as to seem to us something infinitely abhorrent.

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[4] . . . The social insects, their origin and evolution. By William Morton Wheeler. New York, *Harcourt, Brace* and Co., 1928. xviii, 378 p., illus.

DISCUSSION

H. Townes. It seems to me that the aculeate Hymenoptera cannot be derived from the parasitic Hymenoptera. In the Aculeata there are many primitive characters that are not found elsewhere in the Terebrantia. The aculeate hind wing has many veins that are entirely lacking in the Terebrantia. The anal lobe of the Aculeata is entirely lacking in the Terebrantia, except possibly in the Evaniidae. However, in the evaniids there is no proof that the anal lobe is either primitive or homologous with that of the Aculeata. Larvae of the Aculeata, such as that of *Vespa*, have many primitive features not found in the Terebrantia. It seems likely that neither group originated from the other.

J. C. Bradley. Parasitoid and aculeate Hymenoptera must be looked upon as parallel lines, neither derived from known forms of the other but, rather, from common ancestors. The two folds in the hind wing make it clear that the posterior lobe of the Evaniidae is homologous with that of the aculeates.

C. D. Michener. Concerning the interchangeability of animal and plant foods in the Hymenoptera, it may be noted that larvae of some parasitic bees, in the first stage, consume part of the young host larvae, although bees are otherwise entirely phytophagous.

J. C. Bradley. An interesting additional case of food change.

O. W. Richards. Is it wise to rely entirely on wing venation in deciding the relationships of the superfamilies of Clistogastra? Should one not consider also the structure of the thorax and the abdominal spiracles?

J. C. Bradley. Yes; relationships should be decided by knowledge based on all structures.

H. E. Evans. Would you care to comment on the recent paper by Kenneth Cooper who suggests that the Oryssidae may actually feed on fungi in beetle burrows. He points out that it has not been established that they are actually parasites.

J. C. Bradley. The matter seems to be still an open question.

Les Familles des Chalcidoidea (Hymenoptera)

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ABSTRACT

The superfamily Chalcidoidea has been divided by authors into 15 to 20 families, which are not always clearly delimited. With the usual keys, it is generally possible to recognise the main families, but some of the characters considered in the tables may often be confusing.

The broadened hind femora of the Leucospidae and Chalcididae are found also in the Podagrionidae and to a lesser degree in other families. The elongated hind coxae of the Torymidae, the large pronotum of the Eurytomidae, the short and bulging thorax of the Perilampidae and Eucharidae, all these features may also appear in some genera of other families.

After a study of the structure of the thorax in all families and subfamilies, it is our opinion that a better knowledge of the size and sculpture of the pleurae may allow a better classification of the Chalcidoidea. The figure in the text shows the division of the side of the thorax, with the most important parts: the prepectus, which may be more or less developed, the mesopleurae, often divided into episternum and epimeron, and the metapleurae, more or less broadened. Suggestions are made concerning the relations between some of the families.

Le grand ordre des Hyménoptères est actuellement divisé en plusieurs super-familles, groupes naturels, bien définis, qui eux-mêmes sont divisés en familles. Si l'on étudie les Hyménoptères Térébrants, on remarque que les Ichneumonoidea, les Cynipidoidea, et les Proctotrupoidea contiennent chacun un nombre relativement restreint de familles bien distinctes. Les cas sont rares où il y a des doutes sur l'appartenance d'une espèce à telle ou telle famille.

Les Chalcidoidea au contraire sont divisés, suivant les auteurs, en 15 à 20 familles dont les limites et la position sont parfois incertaines. Ce sont en général les anciennes subdivisions de Foerster (1856), revues par Thomson (1875), et un peu modifiées par Ashmead (1904), qui ont été élevées au rang de familles.

La plupart de ces familles sont, avec de l'habitude, facile à reconnaître, mais, dès qu'on se met à analyser les caractères qui servent à les distinguer et qu'on essaie d'établir une bonne table de détermination, on se heurte à des difficultés et des incertitudes. L'élargissement des fémurs postérieurs, qui caractérise les Leucospidae et les Chalcididae, se retrouve chez les Podagrionidae et à un moindre degré dans d'autres familles; les hanches postérieures allongées des Torymidae, le grand pronotum des Eurytomidae, le thorax court et bombé des Perilampidae et des Eucharidae, dont on se sert dans les tables, sont des caractères qui se retrouvent aussi chez certains genres d'autres familles et qui peuvent être mal interprêtés.

Je me suis efforcé de trouver pour chaque famille un ensemble de caractères plus précis en examinant un très grand nombre d'espèces; cependant je ne voudrais attirer l'attention ici, courtement, que sur certaines parties du thorax, dont on n'a, semble-t-il, pas tiré encore tout le parti possible pour la distinction de familles et sous-familles et pour la connaissance de leur parenté.

Dans les descriptions on ne fait mention généralement que de certaines parties du corps, toujours les mêmes. M. Domenichini (1953) a fait faire un pas en avant en publiant une étude détaillée sur la morphologie comparative de l'abdomen chez les chalcidiens et il a pu en tirer plusieurs conclusions intéressantes. Mais il y a une autre partie du corps qui est rarement envisagée et qui donne, à mon avis, des indications précieuses pour la séparation des familles, c'est l'ensemble des pleures sur les côtés du thorax. La structure générale et la division des pièces par des plis ou des sillons sont assez constantes dans une famille pour que l'on puisse classer un insecte même sans examen de la tête, des ailes ou de l'abdomen.

On remarque d'abord que seuls parmi les Hyménoptères parasites, les Chalcidoidea ont un pronotum qui ne s'étend pas ou à peine de côté jusqu'aux tegulae; les propleures sont séparés des tegulae par une pièce spéciale, le prepectus, qui est la partie antérieure de l'épisternum, séparé de celui-ci par une suture complète. La forme et la sculpture des prepectus donnent souvent des indications utiles pour la séparation des genres et des espèces. J'ai montré (Ferrière 1954) l'importance de ces pièces pour la distinction des genres des Eupelmidae et M. Steffan (1952) s'en est servi avec bonheur pour distinguer les espèces du genre *Perilampus*. En comparant les familles, on peut faire les constatations suivantes:

1) Les prepectus sont très petits ou presqu'invisibles chez les Leucospidae, les Chalcididae, et les Eucharidae, ainsi que chez deux sous-familles des Pteromalidae, les Eunotinae et les Metasteninae. Dans ce dernier groupe rentrent non seulement les *Metastenus*, *Dinarmus*, *Picroscytus* et genres voisins, mais encore les genres suivants placés jusqu'ici parmi les Pteromalinae et qui ont tous de très petits prepectus: *Pseudocatolaccus*, *Anisopteromalus*, *Bruchobius*, *Sphaerakis*, *Scymnophagus*, *Neocatolaccus*, et peut-être d'autres encore.[1]

2) Les prepectus sont petits aussi, mais en triangle rectangle, chez les Podagrionidae, les Ormyridae, et les Eurytomidae; chez ces derniers le côté postérieur du triangle est légèrement concave.

3) Ils sont plus grands, triangulaires, plus ou moins allongés en bas chez les Torymidae, les Perilampidae, les Cleonymidae, les Pteromalidae, les Aphelinidae. Les prepectus des Pteromalidae sont parfois plus ou moins enfoncés dans le sillon séparant les propleures des mésopleures.

4) On les trouve très grands et bien visibles chez les Elasmidae, Eulophidae, Tetracampinae, Pireninae.

5) Enfin ils sont grands aussi mais ovales ou plus ou moins arrondis chez les Eupelmidae et les Encyrtidae, ces derniers ayant en outre parfois une lamelle translucide qui recouvre une partie des tegulae et le haut des episternum.

Les *mésopleures* sont le plus souvent divisés en deux parties par un sillon ou un pli oblique, l'épisternum en avant et l'épimeron en arrière; chacune de ces pièces peuvent être elles-mêmes divisées en deux; l'épisternum est parfois séparé de son bord antérieur, que l'on appelle alors le presternum, et l'épimeron peut être formé de deux aires plus ou moins séparées par un sillon transversal ou arrondi, qui sont l'épimeron supérieur et l'épimeron

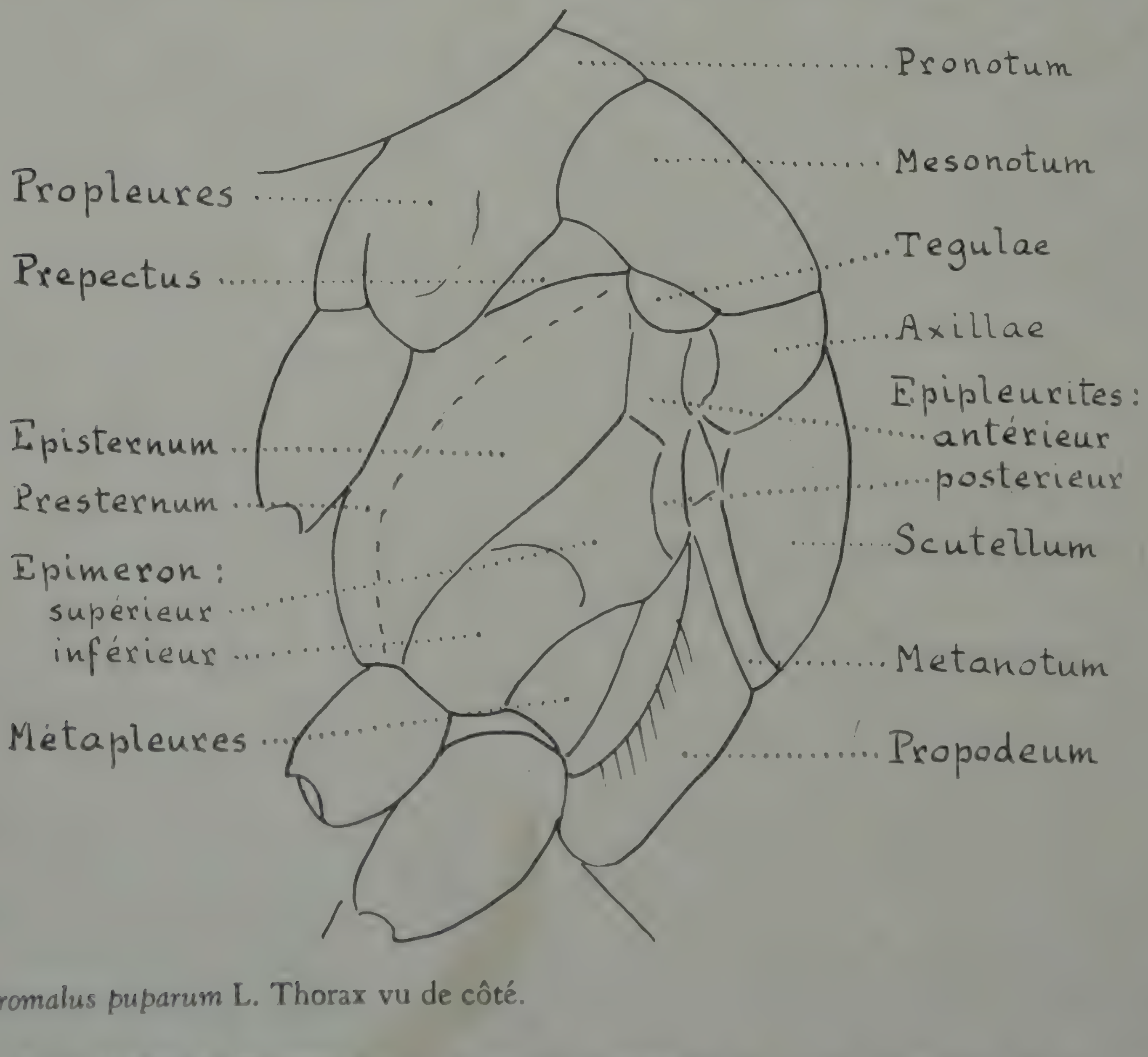

Fig. 1. *Pteromalus puparum* L. Thorax vu de côté.

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[1] Dernièrement (Septembre 1956) M. Delucchi a réuni, en se basant sur d'autres caractères et sans mentionner les prepectus, dans un "complexe Dinarmus", les genres *Dinarmus* (=*Bruchobius* et *Sphaerakis*), *Oedaule*, *Pseudocatolaccus*, *Dinarmoides*, *Paradinarmus*, *Anisopteromalus*, et quelques nouveaux genres. L'examen des prepectus pourrait contribuer à mieux délimiter le "complexe" et en faire peut-être une famille distincte.

inférieur (Fig. 1). Cette division en quatre zones est surtout bien marquée chez les Pteromalidae et les Eulophidae. Chez plusieurs familles l'épimeron n'est pas divisé et est plus ou moins sculpté: Leucospidae, Chalcididae, Podagrionidae, Torymidae, Ormyridae, Eurytomidae, Perilampidae, et Eucharidae. On trouve des mésopleures entiers, sans plis ni divisions, chez les Eupelmidae, Encyrtidae, Spalangiidae, et Eunotinae. Les Aphelinidae ont les mesopleures plats, divisés par trois étroites sutures divergeantes et sont ainsi nettement distincts de tous les Eulophidae. Nous ne pouvons entrer ici dans plus de détails, mais une centaine de dessins des principaux Chalcidiens de toutes les familles nous ont convaincu de l'importance de la structure des mesopleures pour la classification.

Les *métapleures*, au dessus des hanches postérieures, sont aussi de forme et de structure assez constantes dans une même famille. Ils sont très grands et très sculptés chez les Leucospidae et les Chalcididae, grands aussi mais lisses et ovales chez les Podagrionidae. Inversément ils sont très petits, peu visibles, chez les Eupelmidae, Encyrtidae, et Spalangiidae. Entre deux, la comparaison entre la grandeur des métapleures et celle des prepectus peut être souvent utile.

En conclusion nous pouvons dire que l'étude des pleures confirme en général la distinction des familles telles qu'elles sont connues, mais qu'elle donne des indications plus précises que d'autres caractères envisagés jusqu'ici. Les Leucospidae et Chalcididae sont des familles très voisines; les Podagrionidae se rapprochent plutôt des Chalcididae; les Ormyridae sont aussi à séparer des Torymidae, dans lesquels restent les Toryminae, Monodontomerinae, Megastigminae et Idarninae. Les Eupelmidae et Encyrtidae sont très voisins, et les Aphelinidae, avec les mésopleures faiblement convexes et divisés par de fines sutures, ont été avec raison rapprochés des Encyrtidae. Tous les Pteromalidae ont une structure des côtés du thorax très homogène, et ils ne se laissent diviser en sous-familles que par d'autres caractères plus ou moins constants. La plupart des genres placés dans les Cleonymidae sont, à notre avis, à classer parmi les Pteromalidae; par contre certaines sous-familles actuelles pourraient prendre rang de familles spéciales, principalement les Spalangiinae, mais aussi les Eunotinae, les Pireninae, et les Metasteninae.

Je serais heureux que ces quelques remarques ouvrent la voie à des études et comparaisons morphologiques plus complètes de ces pièces du thorax, qui permettront une meilleure classification des familles et sous-familles des Chalcidoidea.

BIBLIOGRAPHIE

Delucchi, V. 1956. Beiträge zur Kenntnis der Pteromaliden, II. *Zeitsch. f. ang. Ent.* 39: 229–257.

Domenichini, G. 1953. Studio sulla morfologia dell'addome degli Hymenoptera Chalcidoidea. *Boll. Zool. Agr. e Bacch.* 19, fasc. 3: 1–115.

Ferrière, C. 1954. Eupelmides brachyptères. *Mitt. Schw. Ent. Ges.* 27: 1–21.

Steffan, J. R. 1952. Les espèces françaises du genre *Perilampus* Latr. *Bull. Soc. Ent. France* 57: 68–74.

DISCUSSION

J. R. STEFFAN. Is there reason to attribute any importance to the pilosity of the thorax?

C. FERRIÈRE. The pilosity of the thorax in the Chalcidoidea has received little study. It is certainly of importance in some large groups, probably in the Microcentri especially.

G. J. KERRICH. Should the Cleonymidae be regarded as a valid family; if so, should it include only the genera closely allied to *Cleonymus* or should *Trigonoderus* and its allies be included?

C. FERRIÈRE. In my opinion the family Cleonymidae should be restricted to the genera allied to *Cleonymus*. Most of the other genera, including those grouped about *Trigonoderus*, are more closely related to the Pteromalidae.

F. I. VAN EMDEN. Is the new grouping of the families in better agreement than the old classification with the larval groups as recognized by H. L. Parker?

C. FERRIÈRE. Larval characters are too poorly known to receive much consideration. The biology and hosts of larvae vary greatly in a single family, and the study of biological characters in relation to morphological characters is not advanced.

Le premier Oviparasite de Psylle et son Hôte *Trioza erythreae* (Del Guercio) au Congo Belge

(Hymenoptera: Chalcidoidea, Encyrtidae; Hemiptera: Psyllidae)

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ABSTRACT

The geographical dispersion of the African citrus psylla, Trioza erythreae *Del G., is very large, from Erythrea to South Africa, through Tanganyika and the Belgian Congo. The synonymy and the noxiousness of this gall-making hemipteron, specific to the rutaceous family, of which six wild host-plants are known, are briefly expounded. Biological control is the best mean of destruction. The first psylla egg-parasite,* Psyllechthrus oophagus *gn. and sp.n. (Encyrtidae: Arrhenophaginae), is described in this paper. Some biological observations have been done on this parasite; the oviparasitism varies from 11 to 96 per cent. This note is also the first record of the Arrhenophaginae form the African continent.*

Avant d'aborder l'étude d'un oviparasite de Psylle, type de parasitisme jamais signalé à ce jour chez ces Hémiptères, je dirai quelques mots de son hôte, *Trioza erythreae* (Del G.) ou psylle des citrus, au sujet duquel j'ai fait incidemment quelques observations biologiques lorsque je le découvris au Congo belge en 1938.

Décrit pour la première fois des cédratiers de l'Erythrée en 1918, par Del Guercio, comme *Aleyrodes erythreae*, ce psylle avait cependant été signalé du continent africain depuis nombre d'années. En effet, en 1899 Rübsaamen décrivait une galle des orangers de l'Afrique du nord qu'il attribuait à un *Trioza sp.*: les pleurocécidies foliaires dont parle cet auteur sont identiques à celles du *Trioza* qui nous occupe aujourd'hui. Puis en 1909, Gowdey retrouvait cette espèce sur les citronniers de l'Uganda et Newstead en 1910 la signalait du Tanganyika, mais ces deux auteurs n'en ont observé que les larves jeunes qu'ils appelèrent "pitted scale larva". En 1922, sans le décrire, Laing dénommait *Trioza citri* ce même insecte récolté au Kenya par Dry: c'est ce binôme qu'utiliseront Waterston (1922) dans son étude sur certains parasites de Psyllides et Thompson (1944) dans ses listes d'entomophages. Puis en 1923, Pettey le redécrivait sous le nom de *T. merwei*, nom que l'auteur placera lui-même en synonymie de *Spanioza erythreae* (Del G.) Boselli (1920). Boselli avait, en effet, transféré l'*Aleyrodes erythreae* Del G. dans sa famille réelle, c'est-à-dire les Psyllidae (=Chermidae), en l'incorporant toutefois dans le genre invalide *Spanioza* Enderlein (1926), lequel fut, par la suite, entièrement assimilé au gn. *Trioza* Foerster (1848) par Tuthill (1943). Cependant, pour la première fois en 1934, Harris cite cette espèce sous son nom exact, soit *Trioza erythreae* (Del G.) dans une étude éthologique sur cet insecte; il est suivi par Ghesquière (1938), Smee (1945), etc.

En résumé, la synonymie de ce psylle s'établit comme suit:

Trioza erythreae (Del Guercio) Harris 1934,	
Trioza sp. Rübsaamen 1899 (descr. cécidie), Psyllidae, Darboux et Houard 1901, Houard 1909 et 1922 (descr. cécidie),	Afrique du nord
Pitted scale larva, Gowdey 1909, Newstead 1910,	Uganda, Tanganyika
Aleyrodes erythreae[1] Del Guercio 1918 (descr. ♀, nymphe et cécidie) (Aleyrodidae), Houard 1922 (taxonomie et cécidie),	Erythrée
Trioza citri Laing 1922 nom. nud. in Waterston 1922 et Thompson 1944 (biologie),	Kenya
Trioza merwei Pettey 1923 (taxonomie), Van der Merwe 1923 (biologie), Pettey 1924 (cécidie), Smee 1933, Silvestri 1939, Boyce 1948 (biologie),	Rhodésie Transvaal Nyassaland

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[1] Sub *Aleurodes eritreae: Aleurodes* Burm. emend. inut. 1835 pro *Aleyrodes* Latr. 1796, *eritreae* = err. typ. évidente que certains auteurs ont reproduite à tort (cf. R. I., art. 19).

Spanioza erythreae Boselli 1930, Pettey 1933 (synonymie), Silvestri 1939, Quayle 1941, Van der Merwe 1941, Grandi 1951 (biologie),	Erythrée Afrique du sud
Trioza erythreae Harris 1934, 1936, Ghesquière 1938 (synonymie et biologie), Rev. appl. Entom., A, 1942 (synonymie), Smee 1945, Ebeling 1951, Hepburn et Bishop 1954, Müller 1956, (biologie).	Nyassaland Congo belge Afrique du sud Rhodésie Tanganyika

Au Congo belge la dispersion de *T. erythreae* est vaste mais sporadique. L'insecte est commun sur les Agrumes cultivés depuis les régions montagneuses du nord du Kivu et du Ruanda jusqu'à la frontière congo-soudanaise, on le trouve dans le Territoire du Ruanda (Rwaza) sur orangers, la Province du Kivu (Rutshuru) sur citronniers, orangers, et bigaradiers, la Province de Stanleyville en Ituri (Irumu) sur orangers et en Haut-Uelé (Aba) sur mandariniers. Au Kivu, et probablement ailleurs aussi, il est fréquent dans les galeries forestières sur trois arbres indigènes: *Clausenia anisata* Oliv. sa plante favorite, *Fagara inaequalis* Engl. et *F. kivuensis* Lebr. Tandis qu'en Afrique du sud, Van der Merwe (1923, 1941) signale *Clausenia inaequalis* Benth. comme hôte préféré, et accessoirement *Fagara capensis* Oliv. et *Toddalia lanceolata* Oliv. Toutes ces plantes appartiennent, comme les agrumes, à la famille des Rutacées à laquelle *T. erythreae* paraît, jusqu'à présent, uniquement inféodé.

Particulièrement néfastes dans les pépinières, les dégâts de ce psylle se manifestent en général par l'apparition, à la partie supérieure des feuilles, de nombreuses petites saillies de 1.5 mm. de diamètre correspondant chacune à une larve aplatie fixée sous le limbe dans la dépression même de la cécidie. La déformation, ou crispation foliaire plus ou moins profonde, qui résulte de ces piqûres s'aggrave notamment de troubles chlorotiques accompagnés, chez les sujets en production, de chute anormale des boutons floraux et des fruits immatures. La nymphose s'opère dans l'excavation larvaire.

Il est curieux de noter que depuis 1899, date de sa première apparition en Afrique septentrionale, le psylle des citrus n'y a plus été signalé, bien que la culture des agrumes se soit depuis lors considérablement développée en ces régions: Trabut (1910), Delassus (1932) et Mimeur (1949) n'en font plus mention. Introduit sans doute de l'Erythrée avec quelque plante d'importation, cet insecte n'aura pu s'acclimater aux chaleurs sèches des étés nord-africains et disparut naturellement des jardins. Un fait analogue a été constaté par Van der Merwe dans le sud-ouest africain où, en raison de certains écoclimats secs et chauds, ce ravageur n'a pu s'implanter dans tous les vergers d'agrumes.

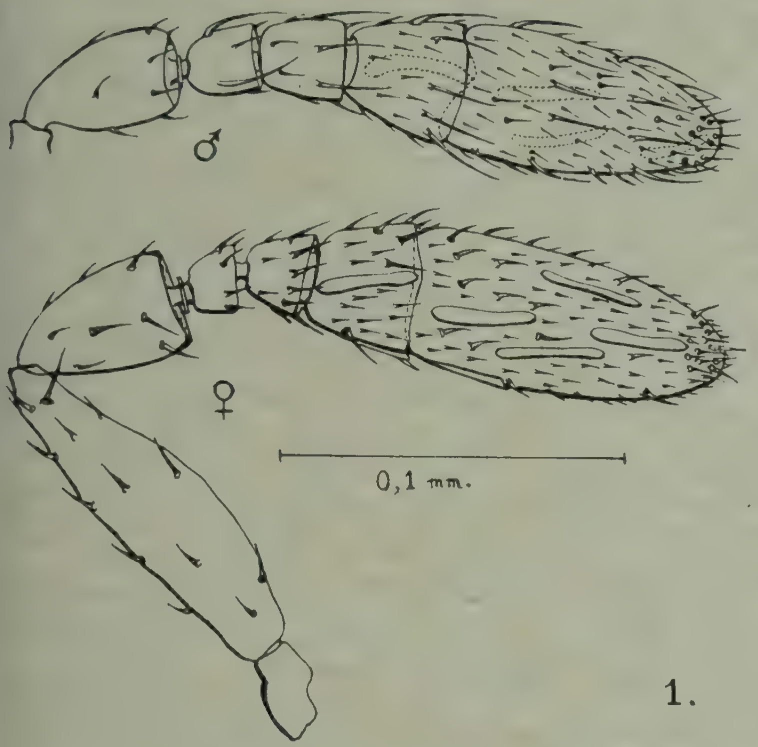
Comme on vient de le voir, le mode de vie de cet insecte exclut pratiquement l'emploi d'insecticides par poudrages ou pulvérisations comme moyen de destruction. En outre, la sporadicité actuelle des vergers d'agrumes sous les tropiques augmente encore les difficultés d'application et le coût des traitements chimiques pour lesquels des appareils à forte pression sont indispensables. La lutte biologique semble donc être la méthode la plus efficace à envisager, mais on ne connaît encore que peu de choses au sujet des ennemis de ce psylle: un syrphide prédateur et deux chalcidiens endoparasites ont été jusqu'à présent signalés en Afrique orientale et méridionale. Je les ai retrouvés tous trois au Congo belge.

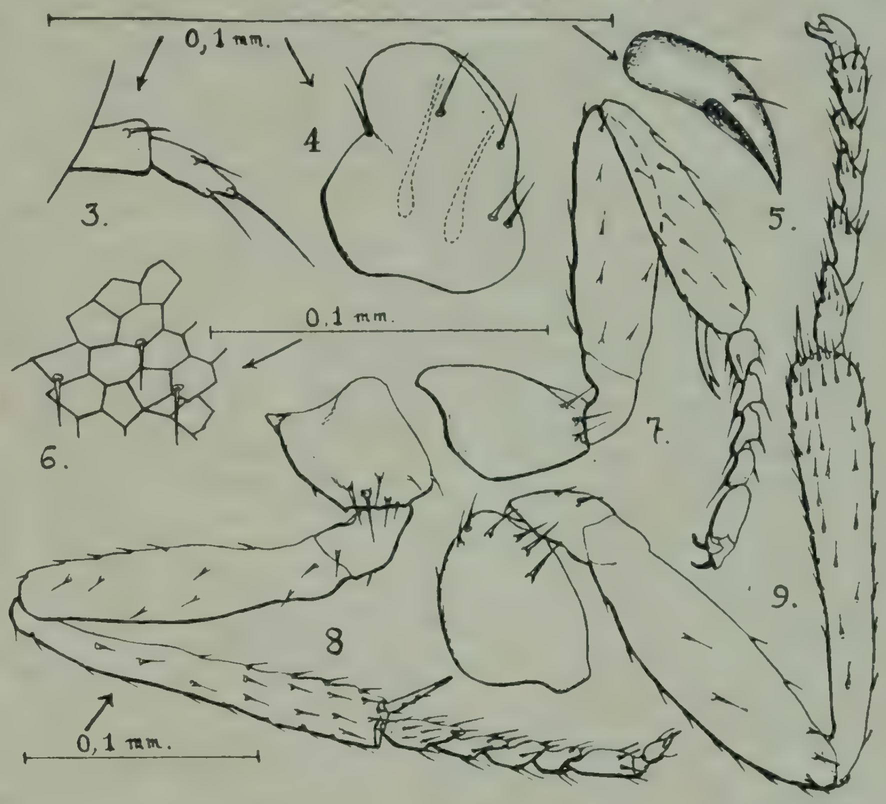
Un fait nouveau, tant au point de vue biologique que taxonomique, est la découverte de l'oviparasite que je décris ci-dessous. Par ses caractères aberrants, cet intéressant auxiliaire présenta tout d'abord quelques difficultés quant à la position systématique à lui attribuer: je l'ai classé parmi les Encyrtidae, Arrhenophaginae.

Le statut de cette sous-famille est en effet assez mal défini. Les genres qui la composent ont entre eux des caractères fondamentaux indiscutables, néanmoins les différences qui les séparent sont telles, que malgré leur petit nombre, on serait tenté de créer une tribu pour chacun d'eux! C'est ainsi que le nouveau genre, objet de cette note, doit être le type d'une tribu nouvelle (Psyllechthrini nov.), à laquelle toutefois je rattacherai un genre de Girault (1915), pour grouper les espèces pentamères, à opposer au groupe des espèces tétramères de cette même sous-famille. Je reviendrai sur cette question ultérieurement.

Genre *Psyllechthrus* nov.

Insectes testacés. Tête: vertex marginé aigu; yeux arrondis, d'un diamètre plus petit que les gêneë; mandibules: face externe à sommet marginé arrondi inerme, vue de profil courbée et aiguë (Figs. 4, 5); palpes maxillaires de deux articles (Fig. 3); antennes insérées sous la ligne oculaire, formule 1.1.1.2.2, scape fusiforme, pédicelle turbiniforme, anneau linéaire, funicule biarticulé à articles obconiques, I plus petit que II, massue biarticulée, ovale-allongée à I obconique, faiblement inéquilatéral, plus long et plus large que le II du funicule, nettement plus petit que le II qui est oblong-elliptique. Thorax bombé aussi large que long, pronotum étroit, mésoscutum à scutum sans parapsides et plus court que le scutellum, métanotum et propodéum étroits. Ailes antérieures oblancéolées, elliptiques, allongées, les cils du bord antérieur nettement plus courts que ceux du bord postérieur, portion distale de la submarginale plus large que la portion proximale, marginale à base plus étroite que le sommet; ailes postérieures étroites, longuement ciliées. Pattes normales, I des tarses plus grand que II, II–III–IV subégaux, V le plus grand égal à III + IV. Abdo-





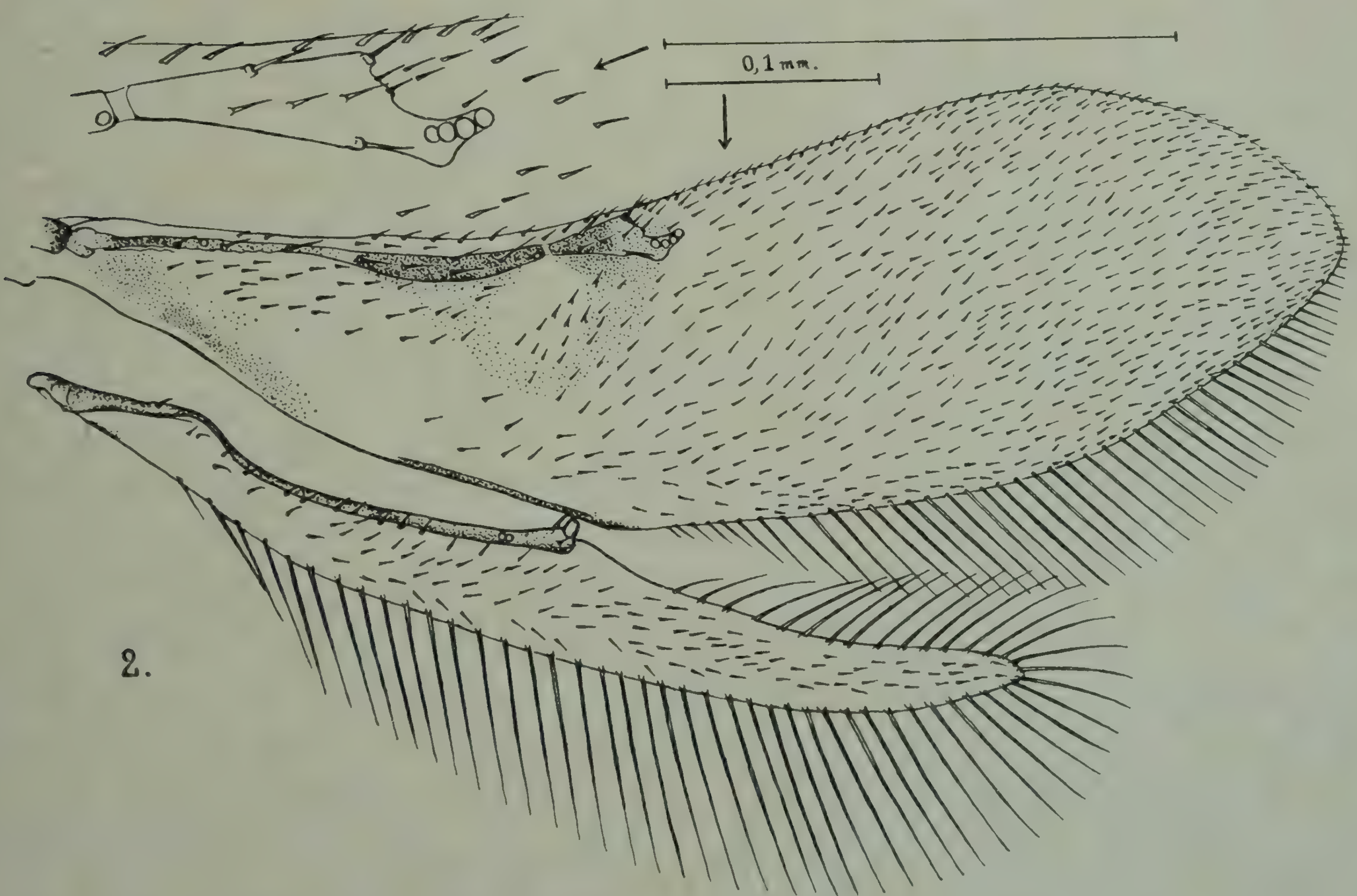


Fig. 1. *Psyllechthrus oophagus* Ghesq., antennes.

Fig. 2. *Psyllechthrus oophagus* Ghesq., ailes antérieure et postérieure. En haut, région marginale fortement grossie.

Figs. 3–9. *Psyllechthrus oophagus* Ghesq. 3, palpe maxillaire; 4, mandibule vue de face; 5, id. vue latérale; 6, réticulation du thorax; 7, patte antérieure; 8, patte médiane; 9, patte postérieure.

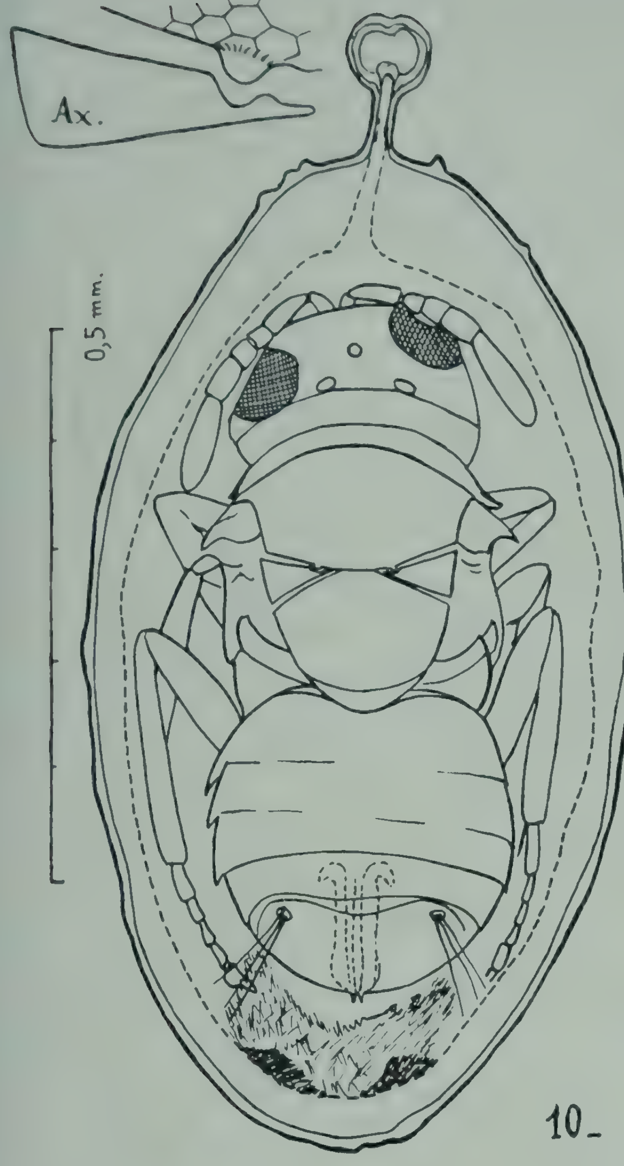
men subarrondi, à peine plus long que large, plaques cercales à vibrisses situées dans le 1/3 apical; tarière peu visible.

Génotype: *Psyllechthrus oophagus* sp. n.

Psyllechthrus oophagus sp. n.

Taille: 0.60 à 0.62 mm. Corps et pattes uniformément brun testacé, sauf la base du scape, le sommet des tibias et les coudes jaune pâle, le V des tarses noirâtre. Ocelles rouges, yeux gris. Ailes antérieures hyalines dans leur portion distale, faiblement enfumées dans leur portion proximale, enfumure d'intensité variable (les taches les plus foncées sont seules indiquées Fig. 2).

♀. Corps, pattes, antennes (scape et pédicelle) et ailes (partiellement) à microsculpture réticulée, en général pentagonale à hexagonale (Fig. 6), isodiamétrale, sauf les pattes, les gênes et les antennes sur lesquelles cette microsculpture s'allonge (1–2 à 1–3); sur les ailes (à sec) une réticulation de plus faible diamètre le long du retinaculum et des nervures. Tête vue de face subarrondie, plus longue que large; fronto-vertex large; ocelles en triangle subéquilatéral, les latéraux distants de l'oeil 1 1/2 fois leur diamètre; yeux petits, arrondis; gênes 2 fois plus longues que le diamètre des yeux. Antennes insérées sous la ligne oculaire; toruli situés à une distance du clypeus égale à leur plus grand diamètre; scape un peu plus court que le sommet de la tête, fusiforme, plus rétréci distalement (Fig. 1), parsemé de quelques cils spinuleux; flagellum claviforme: pédicelle turbiniforme, 1/3 plus long que sa plus grande largeur, nettement plus large et 3 fois plus long que le I du funicule, avec quelques cils spinuleux, anneau très petit mais bien visible; funicule biarticulé à articles dépourvus de sensilles crétiformes, I un quart plus court et plus étroit que II, obconique, inéquilatéral, dans sa portion subapicale une couronne de cils longs et robustes, II de même forme que I mais plus grand et à ciliation un peu plus dense; massue ovale-allongée, biarticulée, chétotaxie comme à la Fig. 1, I obconique, porteur de 3 sensilles crêtiformes, II allongé, 3 fois plus long que I, à base un peu plus étroite que la partie supérieure de I, médialement un peu plus large que I, septum faiblement oblique et ondulé, coté externe avec 4 sensilles crêtiformes, coté interne sans sensilles et à ciliation semblable à celle du côté externe, toute la surface clairsemée de sensilles basiconiques plus densément au sommet. Thorax bombé: pronotum étroit et porteur d'une ligne de cils translucides; mésonotum à scutum plus large que long (3–2), porteur de courts cils translucides très espacés, de chaque côté du bord postérieur 2 petits processus en tubercules s'emboitent dans les encoches correspondantes de la portion apicale des axilles (Fig. 10 Ax.); axilles larges, nettement séparés au sommet, leur écartement égale un tiers de leur longueur; scutellum aussi long que large, arrondi au sommet; métanotum étroit au centre et s'élargissant faiblement latéralement. Ailes antérieures dépassant de la moitié de leur longueur l'apex de l'abdomen, disque 2 fois plus long que large: bord antérieur garni de courts cils plus ou moins espacés, plus courts que les cils du disque; bord postérieur garni de longs cils droits, les plus longs médians, un peu plus courts que la moitié de la plus grande largeur du disque; speculum complet et se prolongeant autour de la stigmale pour atteindre le bord antérieur du disque; disque clairsemé de cils courts, leur écartement dépassant souvent leur longueur; cellule costale étroite dans sa portion distale, plus large que la portion proximale, généralement une douzaine de cils relativement courts, plus nombreux dans la portion distale; nervure submarginale étroite dans sa portion proximale (avec 3 cils et I sensille placoïde), élargie en fuseau dans sa portion distale (avec 5 cils et I sensille placoïde apical), une étroite fenêtre translucide sépare la submarginale de la marginale; marginale oblique n'atteignant pas le bord antérieur du disque, trianguliforme, garnie de 6 cils dont 3 longs et robustes; postmarginale vestigiale; stigmale épaisse, 1/3 plus courte que la marginale, terminée par un bec porteur de 4 sensilles placoïdes et 2 cils basaux au bord externe; ailes postérieures très étroites, falciformes, effilées dans leur moitié distale, la plus grande largeur submédiale, 2 fois plus étroites que le plus long cil, celui-ci 1/4 plus long que le plus long cil des ailes antérieures. Propodéum très étroit médialement, mais plus large que le métanotum latéralement. Pattes: coxas voir Fig. 7, 8, 9; fémurs I un peu plus longs que les tibias, II et III un peu plus courts que les tibias; tibias I subelliptiques, II et III s'élargissant de la base au sommet, éperon médian aussi long que le I du tarse; tarses I plus grands que II, II à IV subégaux entre eux, V le plus épais, égal à III et IV réunis, pulvillus long et épais, aussi long que V, ongles robustes et très courbés, aussi longs que la moitié de V. Abdomen



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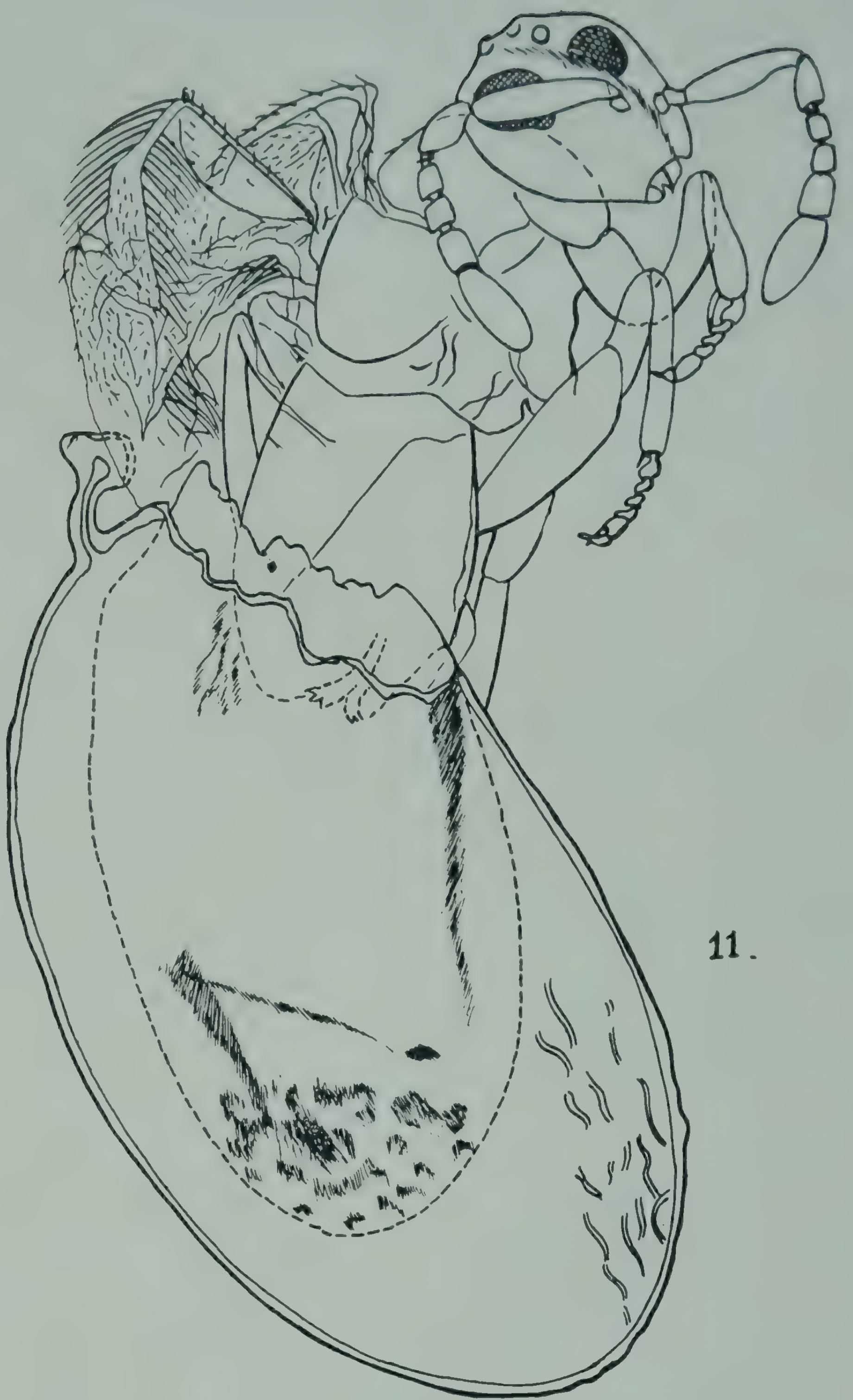

11.

Fig. 10. *Trioza erythreae* (Del G.): oeuf contenant une nymphe de *Psyllechthrus oophagus* Ghesq. ♀ ; Ax: portion scuto-axillaire fortement grossie.

Fig. 11. Éclosion d'un ♂ de *Psyllechthrus oophagus* Ghesq.

arrondi, à peine plus long que large; plaques à vibrisses dans le tiers postérieur; tarière peu visible, sa longueur totale égale le tiers de l'abdomen.

♂. Semblable à la ♀, n'en diffère que par les caractères sexuels secondaires des antennes qui sont un peu plus étroites, à articles de proportions différentes (voir Fig. 1): les I et II du funicule sont plus longs, le I de la massue plus long également, alors que le II est au contraire plus court; la pilosité du flagellum est beaucoup plus longue et les sensilles crêtiformes en nombre moindre.

Congo belge. Province du Kivu: Rutshuru, région montagneuse orientale, 1350 m. alt. environ, 127 ♀ ♀ ♂ ♂ n° 6101, ex oeufs de *Trioza erythreae* (Del G.) sur *Citrus limonum* L., III et IV, 1938, réc. J. Ghesquière.

Holotype, ♀, allotype, ♂, et paratypes au Musée Royal du Congo belge à Tervuren (Belgique).

Des exemplaires de *Trioza erythreae* (Del G.) et de cécidies foliaires sont également déposés dans les collections de cette Institution nationale sous les numéros suivants: 4133, 5578, 6001, 6242, 6243, 6307, 6577, 6606, 6625, 6643, 6652, 6727, 6840.

L'étude biologique de *T. erythreae* n'étant pas, à l'époque, le but principal de mes travaux mais seulement un sujet occasionnel d'observations, je ne l'ai pas recherché spécialement et, de ce fait, les seules pontes parasitées qu'il m'ait été donné de récolter proviennent d'une seule localité.

Comportement et Cycle évolutif de *Psyllechthrus oophagus* Ghesq.

Le parasite se reproduit facilement en captivité. Partant d'une femelle, j'ai, sans difficulté, obtenu deux générations in vitro.

La ♀ gravide circule rapidement sur la face inférieure des feuilles où sont fixés, par un petit pédicule, les oeufs du Psylle. Lorsqu'elle s'approche d'un hôte propice, c'est-à-dire d'un oeuf fraîchement pondu et non parasité, elle s'arrête un instant au pied de celui-ci, le tâte de ses antennes, puis après quelques hésitations, s'achemine vers son sommet qu'elle perfore de sa tarière pour y pondre un unique oeuf.

L'incubation dure 2 jours. A l'éclosion, la larve néonate se tient la tête dirigée vers la base de l'oeuf, elle conservera cette position basipète pendant toute son existence, s'inclinant de droit et de gauche, elle dévore le vitellus et accumule ses déjections dans le vide laissé derrière elle sous la calotte apicale du sac vitellin. La nymphose se passe dans la même position basipète (Fig. 10); sa durée est de 4 à 5 jours. Dès l'achèvement de la métamorphose, l'imago prépare son orifice de sortie en rongeant les parois de la base de l'oeuf à un emplacement presque invariable situé à proximité de l'attache du pédicule. Pour s'échapper, l'imago s'agriffe à la paroi externe du chorion, entrainant dans son effort une partie de la membrane vitelline (Fig. 11). La durée du cycle évolutif (oeuf-imago) oscille de 14 à 18 jours.

In situ, la proportion des oeufs parasités varie entre 11 et 96 pour cent. Comme toujours, ces derniers se distinguent des oeufs normaux par leur teinte plus foncée. Le degré de fécondité des ♀ ♀ n'a pu être établi.

Cette note, première référence relative à la s.-fam. Arrhenophaginae (Encyrtidae) pour le continent africain, est aussi la première contribution au sujet de l'oviparasitisme chez les Psylles.

BIBLIOGRAPHIE

Boselli. 1930. *Boll. Lab. Zool.* 24: 227, Portici.
Boyce in Batchelor et Webber. 1948. *The Citrus Industry* 2: 734, Bekerley.
Darboux et Houard. 1901. *Bull. Sci. France Belgique* 34: III, Paris.
Delassus et autres. 1932. Ennemis des cultures fruitières en Algérie, Alger.
Del Guercio. 1918. *Agric. coloniale*: 168, Figs. 1–3, Florence.
Ebeling. 1951. Subtropical Entomology, 2de éd.: 505, 535, San Francisco.
Enderlein. 1926. *Ent. Mitt. Berlin* 15: 40, Berlin.
Foerster. 1848. *Verh. nat. Ver. preuss. Rheinl.* 5: 67, 82, Aix-la-Chapelle.
Ghesquière. 1938. *Rapp. ann. 1938, Inst. nat. Et. agr. Congo belge*, Ière part.: 51, Bruxelles.
Girault. 1915. *Mem. Queensl. Mus.* 4: 71, Brisbane.
Gowdey. 1909. *Colonial Rpts., Uganda Protect.* n°64: 22, Entebbe.
Grandi. 1951. Introduzione allo Studio della Entomologia 1: 821, Bologne.
Harris. 1934. *Rpt. Dpt. Agric. Tanganyika* (1933): 69, Dar-es-Salam.
Harris. 1936. *E. Afr. agric. Journ.* 1: 498, 4 Figs, Nairobi.
Hepburn et Bishop. 1954. *Bull. Dpt. Agr. U. Sth. Afr.* n° 333: 26, Pretoria.
Houard. 1909. Zoocécidies des Plantes d'Europe 2: 658, Paris.
Houard. 1922. Zoocécidies des Plantes d'Afrique 1: 418, Paris.
Laing. 1922. *in* Waterston (*vid. infr.*).
Mimeur. 1949. Zoocécidies du Maroc, Paris.
Müller in Sorauer. 1956. Handbuch der Pflanzenkrankheiten, 5 éd., 5 (2): 323, Berlin.
Newstead. 1910. *Bull. ent. Res.* 1: 69, Londres.
Pettey. 1923. *S. Afr. Journ. Nat. Hist.* 4: 30, Pretoria.
Pettey. 1924. *Dpt. Agr., Entom. Mem.* n°2: 29, Pretoria.
Pettey. 1933. *Ent. Mem. Dpt. Agric. U. Sth. Afr.* 8 (1932): 19, Pretoria.
Quayle. 1941. Insects of citrus: 56, New York.
Rübsaamen. 1899. *Ent. Nachr. Berlin* 25: 266, Berlin.
Silvestri. 1939. Compendio di Entomologia applicata 1: 385, Portici.
Smee. 1933. *Rpt. Dpt. Agric. Nyassaland*: 50, Zomba.
Smee. 1945. *Rpt. Entom. 1944*, loc. cit.
Thompson. 1944. A catalogue of parasites 1 (3): 112, Belleville.
Trabut. 1910. La défense contre les Cochenilles: 78, Alger.
Tuthill. 1942. *Iowa St. Coll. Journ. Sci.* 17: 548, Des Moines.
Van der Merwe. 1923. *Journ. Dpt. Agr. U. Sth. Afr.* 7: 135, Pretoria.
Vander Merwe. 1941. *Sci. Bull. Dpt. Agr. U. Sth. Afr.* n°233 (Ent. ser. n°8): 5, Pretoria.
Waterston. 1922. *Bull. ent. Res.* 13: 47, Londres.

The Genera of Holarctic Theclinae: A Tentative Revision

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ABSTRACT

This investigation owes its origin to an attempt, inspired by Hemming's "Generic Names of the Holarctic Butterflies" (1934), to give greater precision both to these names and to the concepts that they represent in respect of the hairstreak butterflies. More than a hundred names are involved. Some of these, in their strict application, have nothing to do with the Holarctic fauna and, together with certain homonyms, can be eliminated. Objective synonyms similarly can be rejected. Subjective synonyms and all generic names valid from a nomenclatural point of view have been re-examined as starting points. A wide selection of species has been examined in respect of their external genitalia and re-examined in respect of other characters. Some unsuspected relationships, which appear to be real, have emerged in the process. Some revision of the current 'traditional' classification of the hairstreaks appears desirable, both at generic and supra-generic level. This is discussed. A key to these groups and to the genera is provided.

In examining the generic names of the Lycaenidae in connection with Hemming's *Generic Names of Holarctic Butterflies* (1934), many anomalies were encountered in respect of the application of the names then in current use. These immediately threw into sharp relief many related anomalies in the taxonomic treatment, particularly of the hairstreaks. An initial investigation was based upon an examination of the type species of all the generic names (whether objectively or otherwise regarded as synonyms) at any time employed for any Holarctic hairstreak, the original list being supplied by Hemming. This approach was decided on in the hope that it might provide a short cut to the answers sought and certainly would provide a basis of information concerning the type species at least. The characters first tabulated were only those that could be appreciated without the use of any more elaborate apparatus than a hand lens, such as the venation and shape of the wings, possession and position of tails, the hairiness or otherwise of the eyes and palpi, and especially the shape and condition of the antennae. In 1956 work was resumed and extended to an examination of the male genitalia (only) of all the species originally chosen and of many others.

In the British Isles there occur only five species of hairstreaks, distributed amongst three genera. In Europe proper there are no more than fifteen species, distributed among five genera. These numbers are so small that it is convenient to regard them as a compact unit, the Theclini, without worrying about affinities within the tribe. However, if the whole holarctic region is taken into account it is found that the "hairstreaks", judged on the basis of such popular works as the *Macrolepidoptera of the World*, Holland's *Butterfly Book*, and others, number about 250 species and are distributed among some 40 genera; and their taxonomic treatment often leaves much to be desired. In Seitz, for example, the tribe Polyommatini does not include the genus *Polyommatus*, but consists of coppers and hairstreaks, and the tribe Lycaenini consists of hairstreaks and Polyommatini. A small number of the generic names used in these works can be eliminated at once from consideration since, under the rules of nomenclature, they are based on species that are exotic to the holarctic region. Amongst such names are *Thestor* (formerly incorrectly used for *Tomares*), *Iolaus* (a purely Ethiopian genus), the formerly familiar name of the coppers *Chrysophanus* (the type species of which is *mopsus*, an American hairstreak belonging to the Strymonini), and *Bithys*[1].

The second step in the analysis of the genera of the Holarctic region was to set aside those elements that are in reality invaders from other faunal regions, for example, the neotropical genus *Eumaeus* in North America, the Ethiopian *Epamera* (represented by *E. jordanus* in the Mediterranean subregion), and a number of oriental genera such as *Arhopala*, *Spindasis*, *Chaetoprocta*, *Horaga*, and others in the far eastern sector of the Palaearctic Region. It is this last element, which is so strong in the Far East, that presents the greatest difficulty, for the very large assemblage of oriental genera and species, of which they are but outlying representatives, are themselves urgently in need still of a thorough taxonomic overhaul, though a most valuable contribution to the problem in a limited but very closely related field is to be found in *The Identification of Indian Butterflies* by W. H. Evans (1931). All the oriental genera that invade the Palaearctic areas of China and Japan from India and Burma are soundly characterised and keyed in this extremely useful publication.

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[1] The generic names *Chrysophanus* and *Bithys* are both at present the subject of an application to the International Commission on Zoological Nomenclature, probably involving the use of their Plenary Powers. *Bithys* is used here as if applied strictly in accordance with the Rules, and entirely without prejudice to whatever decision the Commission may reach.

The "coppers", once the unrelated genera such as *Apharitis* and *Cigaritis*, are removed, form a very compact group easily recognised in most cases by their external appearance but much more precisely defined by their characteristic uncus. Viewed in dorsal aspect, the uncus is U-shaped, the rather narrow, widely separated arms being cylindrical and finger-like; seen from the side they might be called sausage-shaped, for they are slightly curved. From the bases of these arms arise the rather delicate falces, which project beyond the extremities of the uncus. The rest of the genitalia display specific variation in great contrast to this constancy of the uncus and falces, but a strongly developed anellus and a large arched penis are characteristic of most species. The tribe was well described otherwise by Scudder many years ago. The oriental genus *Heliophorus* and the very closely related American genus *Iophanus* belong unquestionably to this tribe.

Two other groups, the *Spindasis* group, which is Oriental and African, and the *Aphnaeus* group, which is purely African (though often incorrectly used for certain species of *Spindasis*), can also be easily recognised. The former includes (in so far as the Palaearctic Region is concerned) *Spindasis*, *Cigaritis* and *Apharitis*, the latter *Iraota* and *Amblypodia*. In all of these the hind wing is rather long, tailed, and lobed (except *Cigaritis*) and on the underside (except in *Amblypodia*) silver-marked, the silver usually arranged on a pattern of darker bands. In both groups the uncus is massive and hood-like, the ventral half of the anellus at least is chitinised and is scuttle-shaped, and the valvae are united by their dorsal anterior edges above the penis in a band which may (*Apharitis*) or may not be strongly chitinized. The two groups are readily distinguished by the venational and antennal characters given in the key.

The next group, which may be called the *Iolaus* group, is very characteristic of the tropical regions of the Old World, with relatively few colonists in the Palaearctic Region. To it belong the ethiopian genus *Epamera*, invading the Mediterranean sub-region in a single species, *Epamera jordanus*, and the oriental genera *Dacalana*, *Pratapa*, and *Remelana*. It is an easily recognised group, less easily defined, for it exhibits considerable instability in venation and a wide range of patterns in the male genitalia. Males are almost always mainly brilliant blue above and with prominent secondary sexual characters in the form of hair tufts or patches of modified scales on fore or hind wing or both. The hind wing has a well formed anal lobe and tails at least at veins 1b and 2. The undersides are typically smooth dove-grey, marked marginally with delicate darker lines. The females are like the males but with the brilliant blue replaced by powder blue or grey. In build the species are delicate to moderately robust; antennae with long delicate club, palpi smooth and eyes also (with few exceptions), frons black (sometimes orange) and white; the forewing venation is variable; veins 7, 8 and 9 may all be present, may be reduced to a single vein, but most usually are reduced to 2; veins 6 and 9 (+8 +7) separate, though often very close together at origin. The male genitalia examined show an unusually wide range of characters of specific rather than generic value. The uncus always shows two widely separated lateral lobes, the cleft separating them usually but by no means always, shallow, the lobes extending ventrad in the dorso-ventral plane little more than half way to the median line. The tegumen, otherwise ordinary, in *Britomartis* expands ventrally like a barrel virtually enclosing the claspers; and in *B. cleoboides* the uncus is reduced to negligible proportions and the genitalia as a whole are confined to the dorsal half of the abdomen and enclosed below by two large semi-cylindrical concentric plates, the purpose and origin of which are an enigma. A well formed anellus seems always to be present, except sometimes when, as in *Camena ctesia*, the valvae are completely fused and themselves function as a guide or support to the penis. In so far as the genitalia of this group have been examined, they display a kaleidoscopic variety of specific differences completely unaccompanied at times, at least in the African species, by recognisable external characters.

Before we reach the hard core of the hairstreaks, three other interlopers from the Oriental Region need attention, *Curetis*, *Arhopala*, and *Mahathala*. All three are unmistakable even on superficial characters. The first consists of vividly copper-coloured species with smoothly rounded hind wings and white undersides; the other two contain dull to vivid blue or green species with dull brown undersides marked with slightly darker spots which more often than not are very poorly defined. The male genitalia of all are characteristic. The uncus in *Curetis* is massive, broad, and long, with a single median rather long projection; it is also remarkably shallow, with the falces arising near its base and descending so that their extremities lie between the claspers. The claspers are also relatively large and so deeply cleft as to appear to consist of two claspers on each side. To accommodate these rather massive organs, the lower half of the tegumen is bent back, as it were, into the body, so that in lateral view the tegumen is almost S-shaped. There are rather flat, separated, chitinised anellus sclerites both above and below the penis, the lower one supported on a 'stalk' arising from between the bases of the claspers. *Arhopala* and *Mahathala* are much closer to the true hairstreaks. They have a rather massive, wide, and deep uncus of two lobes separated by a rather wide V-shaped hollow; the socii are strongly developed and are so placed in relation to the ventral extremity of the uncus that the falces (which hinge on both) project backwards and downwards. The best generic character of the genitalia lies in these falces, which are unusually short in both genera, slightly sinuous in *Mahathala*, but perfectly straight in *Arhopala*. The very short middle discocellular vein of the forewing, resulting in the close approximation of veins 5 and 6, is also diagnostic of this group.

From what is now left of the hairstreaks, Sibatani and Ito, in an extremely valuable contribution (only very recently available in Europe), separated off the genera *Antigius*, *Araragi*, *Wagimo*, *Euaspa*, *Catapoecilma*, and *Horaga* as the Horagini. These are, however, a heterogeneous lot having little in common other than that they are not true Theclids or Strymonids. In venation the last two have in common the possession of only 10 veins in the forewing, and they have three slender tails to the hind wings; they also have smooth, hairless eyes; their genitalia could not be more different. In *Catapoecilma* the tegumen is perpendicular, the rather hood-like uncus has a bifid median point, and an anellus is present, in fact the appearance is very Theclid; in *Horaga* the tegumen slopes steeply, the uncus is relatively small, not strongly chitinised and consists of a pair of long very deeply separated lateral lobes, the basal half of the tegumen is greatly broadened and the claspers arise from its ventral border, and there is no trace of an anellus. On genitalia *Horaga* stands widely apart from all the other genera of this tribe; *Catapoecilma*, in spite of the different form of the uncus, appears to show considerable affinity to *Niphanda*, and both seem best placed, possibly in a separate tribe, with *Lycaenesthes* and some related genera.

The remaining four genera, *Antigius*, *Araragi*, *Wagimo*, and *Euaspa*, have much in common. They are similar in wing-shape, in having 11 veins to the forewing, and in having the sexes alike in pattern and coloration. In all the uncus is rather long and bears a prominent median projection, usually in the form of a hook, that may or may not be bifid and which projects well beyond the lateral lobes. The falces do not arise from the posterior extremities of the uncus.

With these four genera there can be associated, because of the similar 'produced' form of the uncus, *Chaetoprocta*, *Drina*, and *Teratozephyrus* (typical section), and the American genera *Hypaurotis*, *Feniseca*, and *Habrodais*. Of these genera only *Feniseca* lacks a tail, and only in the atypical section of *Teratozephyrus* are the sexes dissimilar in the coloration and pattern of the wings. This atypical section, which is the subject of a revision shortly due for publication by my colleague, Mr. Howarth[2], contains species in which the females resemble those of the typical section, but the males are dully metallic green or bluish on the upperside; it is better transferred from this group to the true Theclini. With this atypical section of *Teratozephyrus* one can associate "*Thecla*" *quercus*, the common European Purple Hairstreak on external characters, though its genitalia resemble those of the genus *Favonius*. It is isolated geographically from both genera and has no similarly coloured allies within its own distributional area, so perhaps this combination of characters is not surprising. The generic name *Quercusia* (Verity, 1943) is available for it if considered desirable.

[2] Howarth, T. G. 1957. A Revision of the genus *Neozephyrus* Sibatani and Ito. *Bull. Brit. Mus.* (*Nat. Hist.*) *Entomology* 5: 235–272.

With the reduction of the Horagini to the single genus *Horaga*, it is necessary to form some kind of a group of the other genera now or formerly associated in that tribe. There is, however, such a wide range in the pattern of the genitalia of these genera that grouping them together appears more convenient than natural. Possibly, however, the following subdivisions reflect natural groups:—

1. *Antigius* + *Araragi* + *Wagimo* (only doubtfully separable generically), *Teratozephyrus* (typical section only), *Euaspa*, *Chaetoprocta*, *Hypaurotis*, *Drina* (type species *donina*).
2. *Habrodais*.
3. *Feniseca*.

However, conclusions must wait until it has been possible to examine more of the species in greater detail, and also to relate the genera to their allies in the neighbouring Neotropical and Oriental Regions.

Of the North American genera placed in this group, *Hypaurotis* is of particular interest since it is clearly a derivative of the Palaearctic group containing the species formerly placed in "*Zephyrus*" and "*Thecla*" and now distributed amongst *Teratozephyrus* *Neozephyrus*, *Drina*, and others. Three rare far eastern species, '*Zephyrus*' *atabyrius* Oberthur (1913), '*Zephyrus*' *niveus* Niré (1920), and *Zephyrus kwantungensis* Forster (1942) are particularly close to *Hypaurotis* in the form of their male genitalia. This strongly suggests a distribution similar to that of *Argynnis*, *Ochlodes*, and *Colias*. *Feniseca* is less easy to place but comes closest to the *Coreana* and *Japonica* section. *Habrodais* does not tie in with any Palaearctic genus so far examined, and its relationships are obscure.

The hairstreaks that remain to be considered fall nicely into two well defined groups, the Theclini and the Strymonini. The former are characterised by having, consistently, eleven veins in the forewing and a 'bull-dog' type of genitalia; the latter have consistently ten veins (except for the Old World *Deudorix* group, which has 11 veins) and, to maintain the simile, a 'grey-hound' type of genitalia. Both, fortunately, have type species highly characteristic of the whole group to which they give their names, a situation that does not by any means always arise. In the Theclini the tegumen is perpendicular to the long axis of the body, the uncus is blunt-ended and massive, its lateral lobes descending nearly always to the midline, a well developed anellus is always present and usually also a saccus, the falces are variable and may even be absent, and there is great variety in the form of the claspers, which are almost always movable. By contrast the strymonid tegumen slopes steeply, the uncus is produced in two large lateral lobes which often descend even below the mid line, and the falces are long and delicate, showing little variation. The features of most constant diagnostic value, however, are the lack of an anellus, first pointed out by Sibatani and Ito, and the narrow and relatively small, rather triangular, frequently fused, clasps so placed that they act as a guide to the long (often exceedingly long) penis. Correlated with the long penis there is almost always a very long saccus the purpose of which, presumably, is to provide points of attachment for the muscles controlling the movement of the penis.

Within the true Theclini, to which no northern American species known to me belongs, two or three subdivisions are at once recognisable. In particular one far eastern group is remarkable, in that the male fore tarsus is segmented and clawed. This was first pointed out by Sibatani and Ito, who also transferred to it the genus *Artopoetes* which hitherto had been misplaced in the Polyommatini, but they failed to unite it with *Coreana*, from which the sole species is only specifically distinct. The other subdivisions are : (1) *Thecla*, *Shirozua*, *Laeosopis*, *Neozephyrus*, *Teratozephyrus* (atypical section), *Favonius*, and *Quercusia;* (2) *Amblopala;* (3) *Surendra* (with a remarkably shaped tegumen and a well developed scaphium, unique in the whole of the Theclinae); and (4) *Iratsume*, which shows considerable affinity with the "Horagini" and is quite possibly misplaced here.

In the Strymonini the most surprising thing is the unsuspected extent of the distribution of the group. All the North American hairstreaks, except those of the three genera already dealt with, fall into this group, including *Eumaeus*, and also all the neotropical species so far examined. In the Palaearctic Region *Chliaria*, *Sinthusa*, and the genera allied to *Deudorix* (e.g. *Virachola*, *Rapala*) also fall here. The degree of uniformity displayed by the genitalia throughout the group is remarkable; differences are in the main small and have not at once shown up generic groupings within the Strymonini such as the Theclini present. This situation may change, however, on further study. In the meantime one can readily separate off the Old World Deudorigini by their constant possession of eleven veins in the forewing; *Chliaria* by its lack of a saccus; *Eumaeus* and the rather closely allied genus *Atlides*, at sight, by their heavy build, coloration, thick antennae unmarked by white annulations, and porrect palpi, to form the Eumaeidi, slightly enlarging on Scudder's concept. The remaining genera are less numerous in fact than the number of available generic names suggests and form a fairly homogeneous group which cannot be easily broken up except on rather trifling characters of the antennae and condition of the hind margin of the hindwing. The presence or absence of a small 'brand' at the forewing cell-apex is misleading as a guide to affinities. Generic affinities between east and west are much more apparent in the Strymonini than in any other section of the hairstreaks. *Callophrys*, for example, is definitely Holarctic. So closely allied are *Ginzia* Okanu (*Satsuma* Murray nec Adams) and *Incisalia* on the one hand, and *Nordmannia* and *Erora* on the other, that they are here treated as congeneric. To the nearctic genus *Callipsyche* there appear to belong also three central Asiatic species, *tengstroemi*, *rhymnus* and *cannae*, which were originally described in the old 'omnibus' genus *Thecla*. Almost as nearly related are the Old World genus *Strymonidia* and the New World *Mitoura* and *Calycopis*, the latter separable from each other on little more than secondary sexual characters. The genus *Strymon* itself (type species *melinus*), as understood in these notes, does not occur in the Palaearctic Region or any part of the Old World. The west Palaearctic species of Strymonini, using the same criteria, all fall in the genus *Strymonidia* Tutt (1908), namely *spini*, *w-album*, *ilicis*, *esculi*, *acaciae*, *pruni*, *ledereri*, and *sassanides*, but it should be noted that *w-album*, *ledereri*, and *sassanides* are the type species of certain nominal genera named by Tutt and Strand, which are listed below. *Nordmannia* is available for *myrtale;* but *rhymnus* and *tengstroemi* fall to *Callipsyche*, the type species of which is the American species *bahri*. It is abundantly evident that the tribe Strymonini, with its enormous assemblage of neotropical species, is in serious need of generic revision.

Provisionally the genera discussed in the foregoing notes and indicated in the kev may be arranged in the following tribes:—

1. Aphnaeini
   Amblypodia, Aphnaeus, Iraota.
2. Curetini
   Curetis.
3. Arhopalini
   Arhopala, Mahathala.
4. Eumaeini
   Atlides, Eumaeus.
5. Iolaini
   Epamera, Pratapa, Remelana and Dacalana (venationally aberrant).
6. Theclini (clearly needing further subdivision)
   Amblopala, Antigius, Chaetoprocta, Coreana, Drina, Euaspa, Favonius, Feniseca, Habrodais, Hypaurotis, Iratsume, Japonica, Laeosopis, Neozephyrus, Shirozua, Surendra, Teratozephyrus, Ussuriana, and Wagimo.
7. Deudorigini
   Apharitis, Cigaritis, Deudorix, Lehera, Rapala, Sinthusa, Spindasis, Virachola.
8. Strymonini
   Bithys, Callicista, Callipsyche, Callophrys, Chliaria, Eupsyche, Fixsenia, Horaga, Mitoura, Neolycaena, Nordmannia, Pseudothecla, Satsuma, Satyrium, Strymon, Strymonidia, Tomares.

A postscript. Since the above notes were written and the following key drawn up, a very important and valuable paper on the Theclini by Shirozu and Yamamoto (1956, *Sieboldia* 1: 329–422) has come to hand. These authors' research has led them to notable advances in the taxonomy of this group, being based on a full morphological examination of both sexes of all the species available to them. The six new genera recognised by them (and listed below) run out in the key as follows:—

Protantigius (type species: *superans*) runs out to gen. nov. at couplet 27.

Chrysozephyrus (type species: *smaragdinus*) runs out to *Neozephyrus* from which it is distinguished chiefly by characters of the genitalia.

Howarthia (type species: *coelestis*) runs to *Teratozephyrus*, again distinguished by genitalia.

Revenna (type species: *nivea*) runs out of the key at couplet 34 because forewing MDC is curved and ends at the point of origin of vein 7, thus not falling to either alternative.

Gonerilia (type species: *seraphim*) and *Cordelia* (type species: *comes*) both run to *Chaetoprocta*, from which they differ abundantly in wing venation and genitalia. The characters used to distinguish *seraphim* from *comes* generically, however, do not appear to be of more than specific value. As first reviser I select *Cordelia* in preference to *Gonerilia* (which is misspelt in the text and corrected in the errata) as the name of the genus containing both these species.

KEY TO THE THECLID GENERA OF THE HOLARCTIC REGION

The key to the genera discussed above was prepared as much in the hope of clarifying my own ideas as to their relationships as for any other purpose. It can serve only a preliminary purpose, for very much remains to be done; yet I hope it may prove of some use to those who may take up the study of this very fascinating group of butterflies.

This key is based on males. Though it will be found equally applicable to females in most cases, there are exceptions. The specific names given in the key in brackets after the generic names are those of the type species of those genera. In many cases, but not all, these species alone have so far been critically examined.

1(14) Antennae thickening evenly throughout their length, devoid of white annulations, usually black. Species mostly rather large and robust.
2(7) Forewing with 12 veins.
3(4) Hindwing with small anal lobe and blunt tail at vein 1b . . . . *Amblypodia (anita)*
4(3) Hindwings with filamentous tails at 1b and 2, and anal lobe.
5(6) Forewing veins 5 and 6 from a point, or very close at origin . . . . *Iraota (timoleon)*
6(5) Forewing veins 5 and 6 well separate at origin . . . . *Aphnaeus (orcas)*
7(2) Forewing with less than 12 veins.
8(13) Forewing with eleven veins.
9(10) Hindwing tailless, rounded or sharply angled at vein 4; Forewing vein 7 ends on termen. ♂ copper-coloured, ♀ with white or red discal patch; both silvery below . . . . . *Curetis (thetis)*
10(9) Hindwing lobed and with tail at vein 2; Forewing vein 7 ends at apex.
11(12) Hindwing costa concave . . . . *Mahathala (ameria)*
12(11) Hindwing costa not concave . . . . *Arhopala (phryxus)*
13(8) Forewing with only 10 veins.
Hindwing evenly rounded, tailless . . . . *Eumaeus (minyas)*
Hindwing with anal lobe and tail at vein 2 . . . . *Atlides (halesus)*
14(1) Antennae distinctly clubbed, the club (viewed macroscopically) occupying up to 1/3rd total length of antenna, the shaft with conspicuous white annulations; or, if club not well-defined, shaft at least marked laterally or beneath with white annulations, or whitened, at least basally.
15(16) Forewing with 12 veins . . . . *Dacalana (vidura)*
16(76) Forewing with eleven veins.
17(20) Hindwing evenly rounded, devoid of tails or lobe, but may be scalloped.
18(19) Eyes hairy, palpi smooth. Upperside yellow, heavily black-marked, sexes not dissimilar . . . . *Feniseca (tarquinius)*
19(18) Eyes smooth.
Palpi smooth, fore tarsus segmented and clawed . . . . *Coreana (raphaelis)*
Palpi hairy, fore tarsus simple, spined only, Hindwing margin scalloped, forewing veins 6 and 7 connate . . . . *Laesopis (roboris)*
20(17) Hindwing not evenly rounded, usually with at least one filamentous tail and anal lobe, though any or either may be very short or not strongly developed.
21(22) Hindwing produced at vein 1b to form a rather broad blunt tail . . . . . *Amblopala (avidiena)*
22(59) Hindwing with lobe at anal angle only moderately developed or absent.
23(56) Hindwing with tail or at least a tooth present at vein 2 only (rarely at vein 3).

24(29) Fore tarsus segmented and with claw.
25(28) Palpi very short, projecting less than depth of eye.
26(27) Hindwing tail at vein 2 much less than half as long as vein 2.........*Ussuriana (michaelis)*
27(26) Hindwing tail at vein 2 much more than half as long as vein 2 ....Gen. nov. (for *Drina superans)*
28(25) Palpi normal, much longer than depth of eye.....................*Japonica (saepestriata)*
29(24) Fore tarsus simple, spined.
30(47) Eyes hairy.
31(44) Palpi hairy.
32 (32A) Male fore tarsus sharp ended..................................*Thecla (betulae)*
32A(32) Male fore tarsus blunt ended.
33 (39) Male unlike female (upperside).
34 (38) Male upperside green or blue.
35 (35A) Uncus present..........................*Esakiozephyrus (icana)* [*Teratozephyrus*] partim.
35A(35) Uncus absent.
36 (37) Saccus present...*Neozephyrus (taxila)*
37 (36) Saccus absent..*Favonius (orientalis)*
38 (34) Male upperside silvery.....................................*Iratsume (orsedice)*
39 (33) Male very similar to female (upperside).
40 (41) Hindwing deeply scalloped between veins 2, 3 and 4................*Hypaurotis (crysalus)*
41 (40) Hindwing margin hardly at all concave here.
42 (43) Uncus long, single...*Euaspa (milionia)*
43 (42) Uncus short, spatulate or bifurcate.........................*Teratozephyrus (arisanus)* partim.
44(31) Palpi smooth.
45(46) Fore tarsus short, greatly swollen..........................*Habrodais (grunus)*
46(45) Fore tarsus normal...*Wagimo (signata)*
47(30) Eyes smooth.
48(49) Palpi hairy..*Chaetoprocta (odata)*
49(48) Palpi smooth.
50(51) Forewing veins 6 and 7 (+8 +9) stalked.......................*Shirozua* (jonasi)
51(50) Forewing veins 6 and 7 connate or 7 (+8 +9) arising before cell end.
52(53) Forewing veins 6 and 7 connate..............................*Drina (donina)*
53(52) Forewing vein 7 (+8 +9) arising before cell end.
54(55) Antennae white-marked beneath only, sexes dissimilar..............*Surendra (quercetorum)*
55(54) Antennae white-ringed, sexes alike...........................*Antigius (attilia)*
56(23) Hindwing with tail or at least a tooth at vein 1b as well as vein 2.
57(58) Forewing termen slightly concave below vein 5...................*Apharitis (epargyros)*
58(57) Forewing termen evenly rounded...............................*Cigaritis (zohra)*
59(22) Hindwing with strongly developed anal lobe.
60(69) Hindwing with filamentous tail at vein 2 only (Deudorigini: ♂ genitalia Strymonine).
61(62) Forewing vein 7 (+8 +9) arising about opposite end of vein 10 .....*Sinthusa (nasaka)*
62(61) Forewing vein 7 (+8 +9) well before end of vein 10.
63(64) Hindwing tail at vein 2 much longer in ♀ than ♂; underside green.....*Lehera (eryx)*
64(63) Hindwing tail at vein 2 equally long in both sexes, underside not green.
65(66) ♂ without secondary sexual characters..........................*Deudorix (epijarbas)*
66(67) ♂ with patch of modified scales near base of vein 7 on hindwing above and usually hair tuft mid-dorsum on underside of forewing.
67(68) Forewing veins 6 and 7 from a point............................*Virachola (perse)*
68(67) Forewing veins 6 and 7 separate at origin........................*Rapala (varuna)*
69(60) Hindwing with filamentous tails at veins 1b, 2 and sometimes 3.
70(71) Forewing veins 6 and 7 (+8 +9) forked or from a point. Stout species, underside traversed by dark bands enclosing silvery markings..............................*Spindasis (natalensis)*
71(70) Forewing veins 6 and 7 (+8 +9) separate.
72(75) Rather delicate species (mainly), ♂ upperside blue, ♀ powder blue, underside usually dove grey or brown with markings of delicate lines, devoid of conspicuous metallic markings. ♂ usually a hair pencil on dorsum of forewing beneath or elsewhere, and patches of modified scales............ *Iolaus* group
73(74) Forewing veins 6 and 7 from a point at cell end...................*Epamera (glaucus)*
74(73) Forewing vein 7 before cell end..............................*Pratapa (deva)*
75(72) ♂ purplish blue above, underside reddish brown with conspicuous metallic markings on hindwing between vein 5 and inner margin. ♂ genitalia Strymonine...........*Remelana (jangala)*

76(16) Forewing with 10 veins only (Strymonini).
77(88) Palpi smooth.
78(87) Hindwing lobed and tallied.
79(80) Forewing vein 7 from or beyond cell end........................*Dolymorpha (jada)*
80(79) Forewing vein 7 before cell end.
81(87) Hindwing with filamentous tail at vein 2 and tooth or short tail at vein 3.
82(85) Antennal club rather gradual.
83(84) Antennal shaft imperfectly white ringed........................*Bithys (leucophaeus)*
84(83) Antennal annulations complete................................*Eupsyche (m-album)*
85(82) Club abrupt, about 1/5th as long as shaft ♂ upperside not blue......*Strymon (melinus)*
85(81) Hindwing with filamentous tails at veins 1b and 2, not at vein 3.....*Chliaria (othona)*
87(78) Hindwing without lobe or tail; ♂ with brand mid-costa forewing....*Callicista (ocellifera)*
88(77) Palpi hairy.
89(106) Hindwing without tails.
90(93) Hindwing hind margin crenulate.
91(92) Hindwing with anal lobe......................................*Ginzia (ferrea)*
92(91) Hindwing with tooth only at end of vein 1b.......................*Callophrys (rubi)*
93(90) Hindwing margin evenly rounded, at most a small projection at anal angle or vein 2.
94(103) Antennal club (nudum + 2 segments) less than 8 times as long as wide.
95(96) Forewing veins 6 and 7 (+8 +9) stalked.......................*Tomares (ballus)*
96(95) Veins 6 and 7 separate.
97(100) Male with androconial stigma at anterior end of cell.
98(99) Forewing MDC distorted by stigma............................*Fixsenia (herzi)*
99(98) Forewing MDC at right angles to vein 6........................*Callipsyche (behrii)*
100(97) Male without stigma.
101(102) Hindwing margin very faintly projecting at anal angle and vein 1b....*Nordmannia (myrtale)*
102(101) Hind margin smoothly rounded...............................*Satyrium (fuliginosum)*
103(94) Antennal club at least 8 times as long as wide.
104(105) Eyes smooth..*Neolycaena (sinensis)*
105(104) Eyes hairy...*Pseudothecla (lunulata)*
106(89) Hindwing tailled, or at least with a prominent tooth at vein 2.
107(108) Eyes smooth..*Horaga (onyx)*
108(107) Eyes hairy.
109(110) Antennal club not more than three times as broad as shaft at 2/3rds, club gradual.............. *Strymonidia (thalia)*
110(109) Antennal club more than three times as broad as shaft at 2/3rds, club arising abruptly.......... *Mitoura (smilacis)*

DISCUSSION

A. B. Klots. Can you discuss the relationship of *Feniseca* to the Gerydinae and Spalginae? The relationships of *Erora* can, perhaps, be determined from its unusual larva characters.

N. D. Riley. The similarity in habits of *Feniseca*, *Gerydus*, and *Spalgis* is not correlated with any morphologic characters of taxonomic significance so far discovered. This seems to be a case of parallelism in habits that is independent of affinity. Larval characters of *Erora* may prove useful in elucidating affinities. However, the affinities, now evaluated on the basis of adult structure, lie with certain Asiatic species of which the life histories are unknown, *Nordmannia*, for example.

The Genera of the Australian Tortricidae (Lepidoptera)

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ABSTRACT

The generic classification of the Australian Tortricidae is briefly reviewed. Employed for the first time are genitalic characters, as well as the other characters which Meyrick (1910, 1913) relied upon entirely. The female signum, used by Pierce and Metcalfe (1922) to distinguish the major groups of the British genera, has proved of limited value, especially in placing the more specialized genera. Five important phylogenetic lines are recognised in the Australian Tortricidae.

The Tortricinae, the Cnephasiinae, and the Archipinae, the three major groups of Pierce and Metcalfe, are all represented in the Australian fauna. To the Cnephasiinae have been assigned a group of genera related to Arotrophora *Meyr. and* Taeniarchis *Meyr., mainly of Oriental and Australian distribution. The Schoenoteninae, recently raised to family status by Diakonoff (1952b), probably stem from these Cnesphasiinae, in many of which M is present in the cell of the forewing. The Zacoriscides or Zacoriscini of Diakonoff (1941, 1952a) are apparently specialized forms of the Archipinae and may not deserve subfamily rank. To the Archipinae belong most of the numerous species Meyrick referred to* Tortrix *Linn. A new subfamily is proposed for a rather homogeneous group of genera correlated to both the Cnephasiinae and the Archipinae. It includes many Australian species erroneously assigned by Meyrick to the genera* Capua *Steph.,* Homona *Walk.,* Cacoecia *Hübn.,* Eulia *Hübn.,* Tortrix *Linn., and* Batodes *Guen., together with certain endemic and Papuan genera such as* Rhomboceros *Meyr.*

The author discusses characters used for the separation of the subfamilies and includes notes on the synonymy and geographical distribution of the genera.

No major revision of the Australian Tortricidae has appeared since Meyrick's (1913) review of the world fauna. The classification in that review is based almost entirely on the earlier revisions of Meyrick (1881, 1910). Characters of the genitalia, used effectively by Pierce and Metcalfe (1922) and Obraztsov (1954, 1955) for the Palearctic fauna and by Diakonoff (1939, 1952b–55) for the Oriental and Papuan species, were not considered by Meyrick and other Australian workers. The marked development of this family in the Australian Region renders a study of the genera and their affinities of special interest. The preparation of a detailed revision of the Australian species has made it possible to present this brief review of the generic classification.

Pierce and Metcalfe (1922), attributing special importance to the signum of the female genitalia, distinguished three major groups, the Archipidii, the Cnephasidii and the Peroneidii. This character, if used alone, has proved of only limited value for the delineation of major groups in the Australian and Papuan faunas. Characters of both the male and female genitalia, when considered in conjunction with other characters, have led to the conclusion that the Australian Tortricidae have developed along five important phylogenetic lines. The five resultant groups can conveniently be exemplified in the Australian fauna by *Arotrophora* Meyr., *Eboda* Walk., *Schoenotenes* Meyr., *Epitymbia* Meyr. and *Homona* Walk. These groups are here considered to have subfamily status.

Three of these groups correspond to those distinguished by Pierce and Metcalfe. *Eboda* belongs to the Peroneidii or Tortricinae, and *Homona* to the Archipidii or Archipinae. The Cnephasidii or Cnephasiinae are represented in the Australian Region by a group of genera allied to *Arotrophora*. *Schoenotenes* and certain allied genera have been given family status by Diakonoff (1952a), while *Epitymbia* represents a group of Australian and New Guinea genera which does not fit readily into the other subfamilies.

CNEPHASIINAE

Arotrophora and several endemic genera exhibit many characters which indicate a relationship to the Palearctic genus *Cnephasia* Curtis. However the specialized "floricomous" ovipositor characteristic of *Cnephasia* is absent in the Australian genera.

In *Arotrophora* Meyr., *Taeniarchis* Meyr., *Parastranga* Meyr., *Paranepsia* Turn., *Mictoneura* Meyr., *Drachmobola* Meyr. and *Polylopha* Low., the stem of M is present or partially developed in the cell of the forewing (Fig. 1). Basally it is parallel and closely approximated to R, but near the base of R_1 curves obliquely across the cell to end between the bases of M_2 and M_3. Diakonoff (1939) has figured it clearly in *Taeniarchis*, but has omitted it from *Arotrophora* in which it is also well developed. A similar strong M in the cell of the forewing is found in most of the Schoenoteninae and in some genera of the Ceracinae, a subfamily not recorded from the Australian continent. In the more specialized species of *Arotrophora* and in *Paraphyas* Turn., *Apura* Turn. and *Aeolostoma* Meyr., the stem of M has disappeared entirely.

Pierce and Metcalfe (1922) distinguish their group Cnephasidii by the signum of the female bursa copulatrix which, in the British species, is a dentate band. Obraztsov (1955) has greatly expanded this definition and with few exceptions the Australian genera conform to this wider definition. In the Australian genera the signum is usually an oval scobinate or dentate patch. The three small genera *Aeolostoma*, *Drachmobola* and *Paraphyas* have paired signa, a normal character in the Olethreutidae, but appearing independently in a few tortricid genera.

The socii of the male genitalia are large and drooping in *Arotrophora* and closely related genera, but in the more specialized species are often much smaller. The uncus, as in *Cnephasia*, is long and slender and is devoid of the dense brush of hairs beneath the apex characteristic of the Archipinae, the Ceracinae and the genera allied to *Epitymbia*. It is however bifurcate in the more specialized species of *Arotrophora*, whilst in *Mictoneura* the uncus is spatulate near the apex though slender at the base.

In addition to the genera mentioned above, *Lophoprora* Meyr. from New Guinea and *Terthreutis* Meyr., *Pternozyga* Meyr. and *Prototerpna* Meyr. from India belong here. Diakonoff (1939) shows that the stem of M is present in the forewings of each of these genera and, in a reduced condition, even in the Palearctic genus *Eulia* Hübn. Obraztsov (1955) figures the forewings of two other Palearctic genera, *Olindia* Guen. and *Doloploca* Hübn., with a partially developed M. The figured genitalia of all these genera are characteristic of the Cnephasiinae.

TORTRICINAE

The subfamily is well developed in the Holarctic but relatively few genera occur in the Oriental and Australian Regions. Only four have been recorded from Australia: *Eboda* Walk., *Phricanthes* Meyr., *Scolioplecta* Meyr. and *Tymbarcha* Meyr. As only the unique female type of *T. glycera* Meyr. from Australia is known, it remains doubtful whether it is in fact congeneric with the Indian *T. cerinopa* Meyr., the type species of this genus.

The genitalic characters of the subfamily have been well described by Diakonoff (1939) and Obraztsov (1955). Of special diagnostic significance is the absence of the uncus in the male. The stem of M is seldom if ever developed, the gnathos is usually greatly reduced and the valvae are simple or have a specialized distal brachiola. The signum is usually absent in the Australian genera.

SCHOENOTENINAE

The subfamily has reached its greatest development in the Papuan sub-region (Diakonoff 1954) and is represented in Australia by only a few species of *Schoenotenes* and two smaller genera *Palaeotoma* Meyr. and *Proselena* Meyr. *Paraselena* Meyr. is a synonym of the latter.

Family status for the group does not appear to be warranted for most of the diagnostic characters listed by Diakonoff (1952b, 1954) also appear independently in other subfamilies of the Tortricidae. The strong stem of M in the cell of the forewing is found in several genera of the Cnephasiinae and in the Ceracinae. The sparse scaling of the underside of both wings, and the contrasted prominent scaling of the veins, is present in certain species of *Adoxophyes* in the Archipinae; in *Taeniarchis* and *Drachmobola* in the Cnephasiinae and in *Phricanthes* and *Scolioplecta* in the Tortricinae this character is present but less prominent. On the other hand, it is absent in *Proselena* and *Palaeotoma* placed by Diakonoff in the Schoenotenidae. The tufts of raised scales in the forewing of many species of Schoenoteninae also occur in some of the Tortricinae, Cnephasiinae and even in *Argyrotoxa pompica* Turn. and *Cnephasia sulfurosa* Meyr., both of which must be referred to the Archipinae. The genitalia of the Schoenoteninae are typically tortricoid, as stated by Diakonoff, though in many species they show considerable specialization.

EPITYMBIINAE SUBFAM. NOV.

Uncus narrowly or broadly spatulate, with apex often pointed, a dense brush of hairs beneath apex; socii large or moderate, but reduced in many specialized forms; transtilla sometimes membranous, usually strongly sclerotized, without dense spining on upper surface; valvae sometimes asymmetrical, usually strongly sclerotized, sacculus often ornamented with various projections or spines; aedeagus heavily sclerotized, often ornamented. Female with copulatory orifice and often the 7th. abdominal sternite heavily sclerotized, often intricately formed and sometimes asymmetrical, colliculum entire and fused to ostium, cestum absent; signum a dentate patch or ridge, a sclerotized plate or a tapering spine without capitulum.

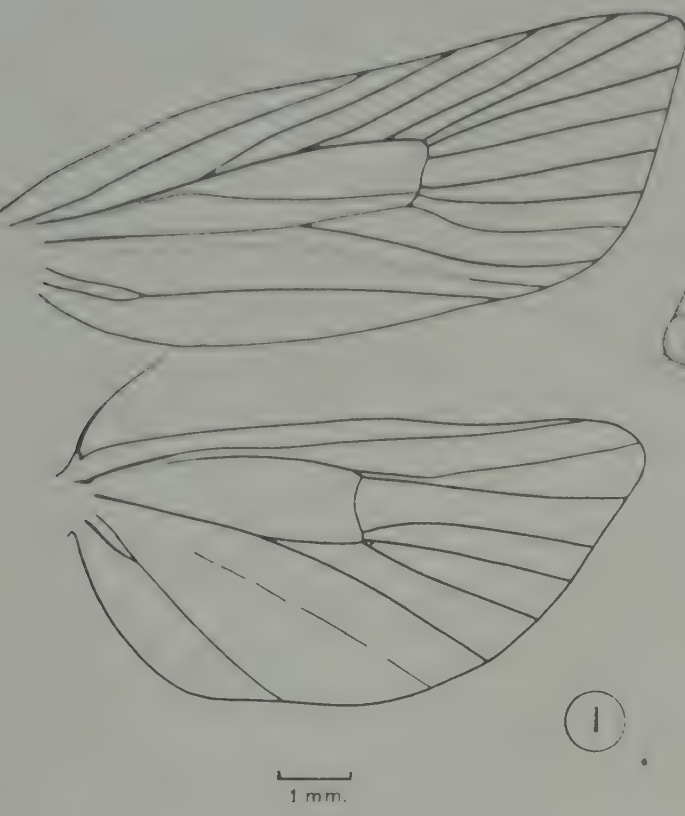
This new subfamily is proposed for a group of genera allied to *Epitymbia* Meyr. which shows certain affinities with both the Cnephasiinae and the Archipinae. From both of these subfamilies the genera may be distinguished by the heavily sclerotized genitalia and the ornamentation of the sacculus and aedeagus in the male (Figs. 2, 3). In addition, the spatulate uncus with a dense brush beneath the apex does not occur in the Cnephasiinae. In the female the heavily sclerotized, intricate and often asymmetrical copulatory orifice (Fig. 4) distinguishes the subfamily from both the Cnephasiinae and the Archipinae. The form of the female signum varies from a dentate patch to a tapering spine without capitulum even in genera which are clearly closely related.

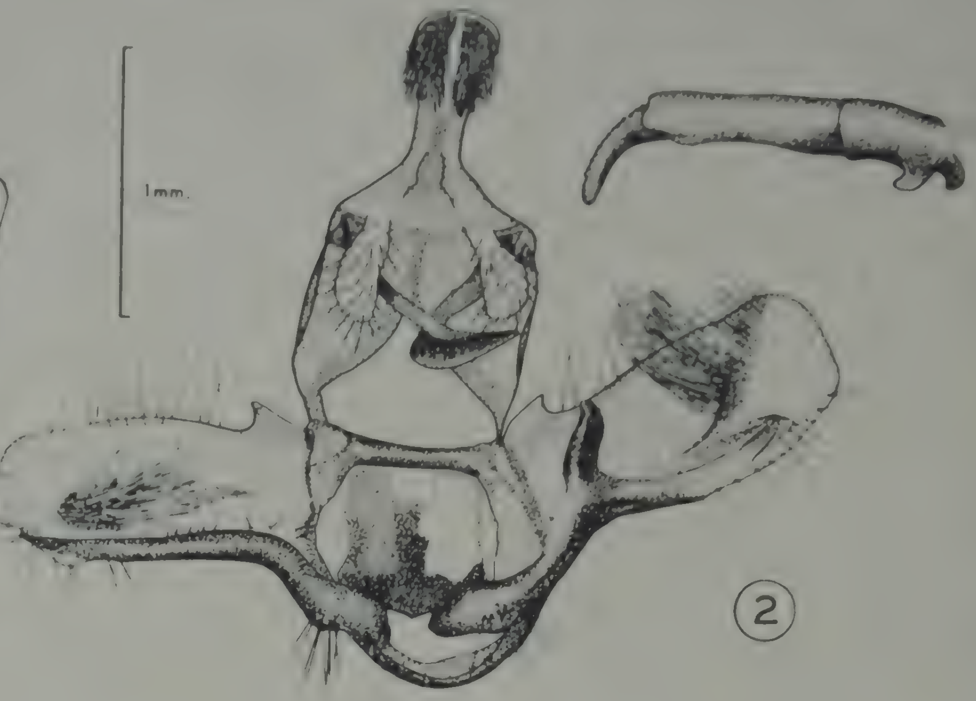
Five of the fifteen Australian genera are segregates of the large group of species placed by Meyrick in *Capua* Stephens. *Epitymbia*, for example, has been reinstated to contain four species showing an extraordinary sexual dimorphism, which previously led to much confusion not only in determining their generic assignments but in correctly associating the sexes of any one species. The female of *E. alaudana* Meyr., the type species, was described by Meyrick as *Capua periopa*, whilst Turner later redescribed it as *Capua cydropis*. Meyrick described males of a second closely allied species as *Isochorista cosmota*. The females, described as *Pyrgotis callizyga* Low., he regarded as distinct but congeneric, whereas Turner based a new genus *Anisochorista* on this female. Finally Meyrick erroneously associated the female of a third species, *Dichelia scotinopa* Low., with the male of his *Capua ophthalmias* which belongs to the Archipinae.

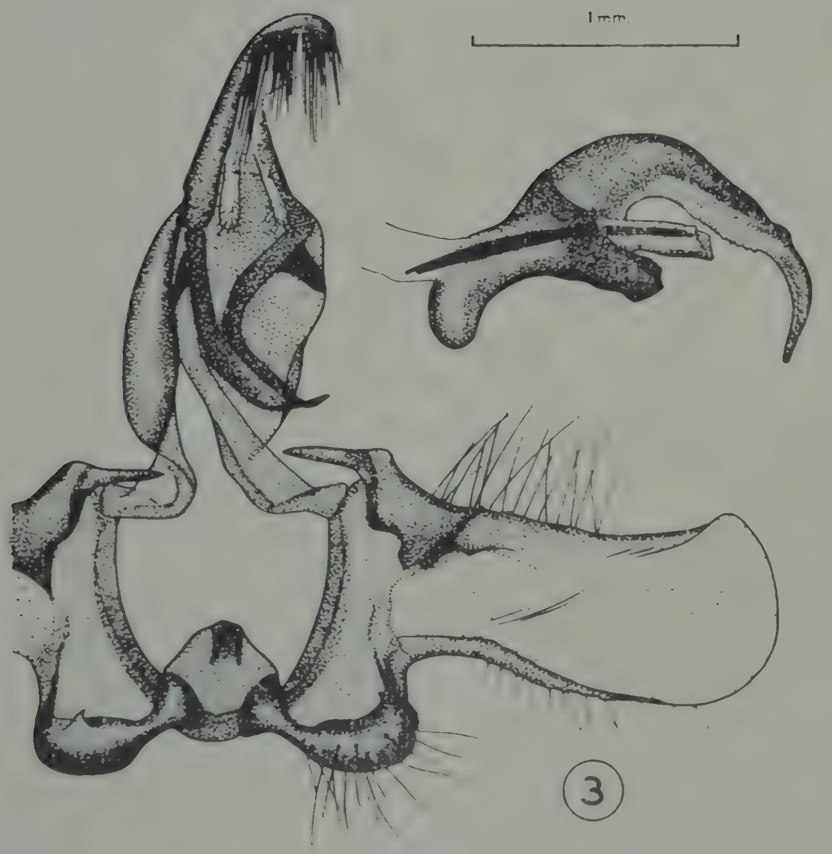
Anisogona Meyr. has been reinstated to include several species previously assigned by Meyrick and Turner to *Homona* Walk. *Anisogona* and *Epitymbia*, together with *Meritastis* Meyr. and certain undescribed genera form a compact group with moderate to small socii in the male and with the signum in the form of a dentate ridge or patch or a spine. In one small genus the signa are paired, dentate ridges.

A second compact group includes *Rhomboceros* Meyr., which occurs also in New Guinea, and the three endemic genera *Asthenoptycha* Meyr., *Capnoptycha* Meyr. and *Trychnophylla* Turner. Previously *Asthenoptycha* has been synonymised by Meyrick with the Palearctic *Batodes* Guen. Though *Capnoptycha* is usually associated with rain forest in eastern Queensland and may therefore also occur in New Guinea, *C. thelea* Diak. is not congeneric, but is more nearly related to *Rhomboceros*. The latter was based on *R. nodicornis* Meyr. from Sariba Island, near the eastern tip of New Guinea. Meyrick failed to recognise the female, which superficially resembles a small *Homona*, and described specimens of it from St. Aignan Island and north Queensland as *H. homogama*. Queensland specimens appear to be conspecific with the holotype of *R. nodicornis*. *Rhomboceros* and the related Papuan genera *Aplastoceros* Diak., *Mimeoclysia* Diak., *Cleptocaca* Diak. and *Pandurista* Meyr. have been referred to the Cnephasiinae by Diakonoff (1953).

Capua euphona Meyr. and several related species form perhaps the most interesting group of the Epitymbiinae. In the female the seventh abdominal somite bears a dense brush of long scales which largely surrounds the lobes of the ovipositor and the sclerotized copulatory orifice. These scales appear to be homologous with the corethrogyne scales which Diakonoff (1952a) regarded as diagnostic for his tribe Zacoriscini (Figs. 6, 7). However, the female signum is a patch of fine dentations which, together with the heavily







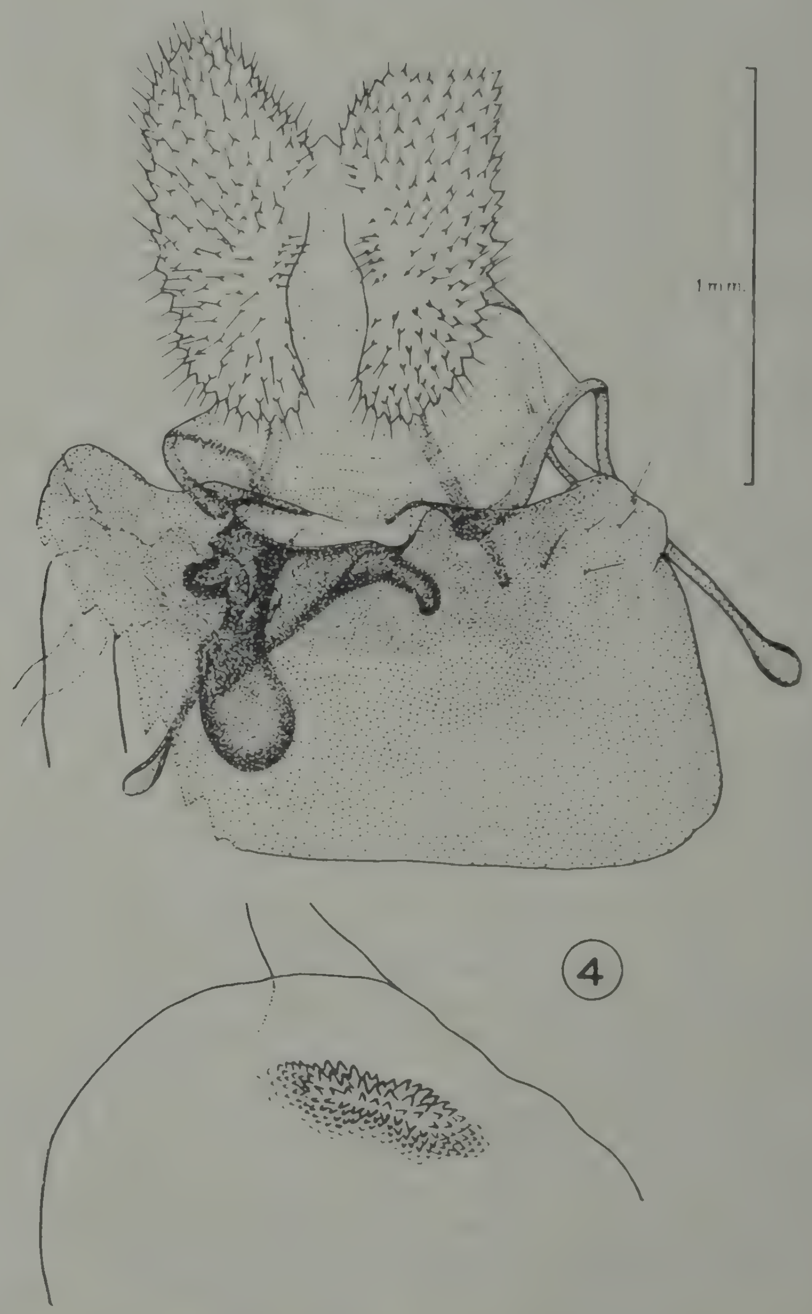


Fig. 1. Venation of *Arotrophora arcuatalis* (Walk.), showing development of stem of M in cell of forewing (sub-family Cnephasiinae).

Fig. 2. Male genitalia of *Epitymbia alaudana* Meyr., type species of genus *Epitymbia* Meyr. (subfamily Epitymbiinae).

Fig. 3. Male genitalia of *Cacoecia lythrodana* Meyr. (subfamily Epitymbiinae).

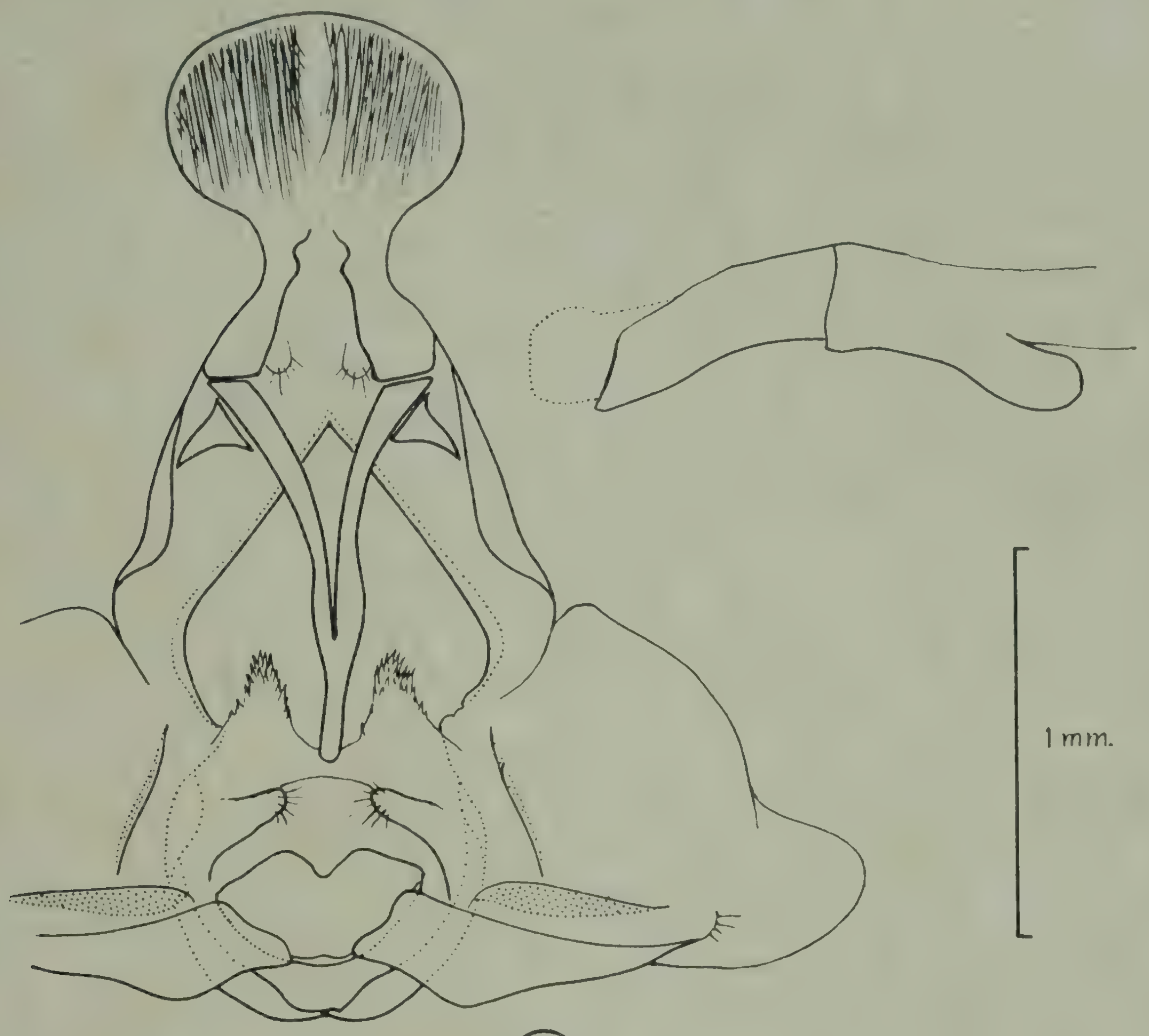
Fig. 4. Female genitalia of *Epitymbia alaudana* Meyr. (subfamily Epitymbiinae).

sclerotized and serrate sacculus bearing strong spines and the curiously formed orifice of the aedeagus in the male, indicates a relationship to the other genera of the Epitymbiinae.

ARCHIPINAE

Most of the Australian and probably all the New Zealand Tortricidae belong to the Archipinae. The valva of the male is simple, the sacculus is seldom heavily sclerotized but sometimes ends in one or two simple thorns, the upperside of the transtilla when present is usually covered with short spines, the socii are sometimes large but are more usually moderate to small and, in several genera, a mensis ventralis is present. The split colliculum and the cestum often found in the female do not occur in the other Australian subfamilies, while the signum may be a thorn, a straight or curved tapering spine, a strong hook or a dagger with a serrated blade. A capitulum, which is often present, is also diagnostic.

Whereas specialization in the genitalia of the Epitymbiinae has resulted in a heavy sclerotization and ornamentation of the sacculus, the aedeagus and the female copulatory



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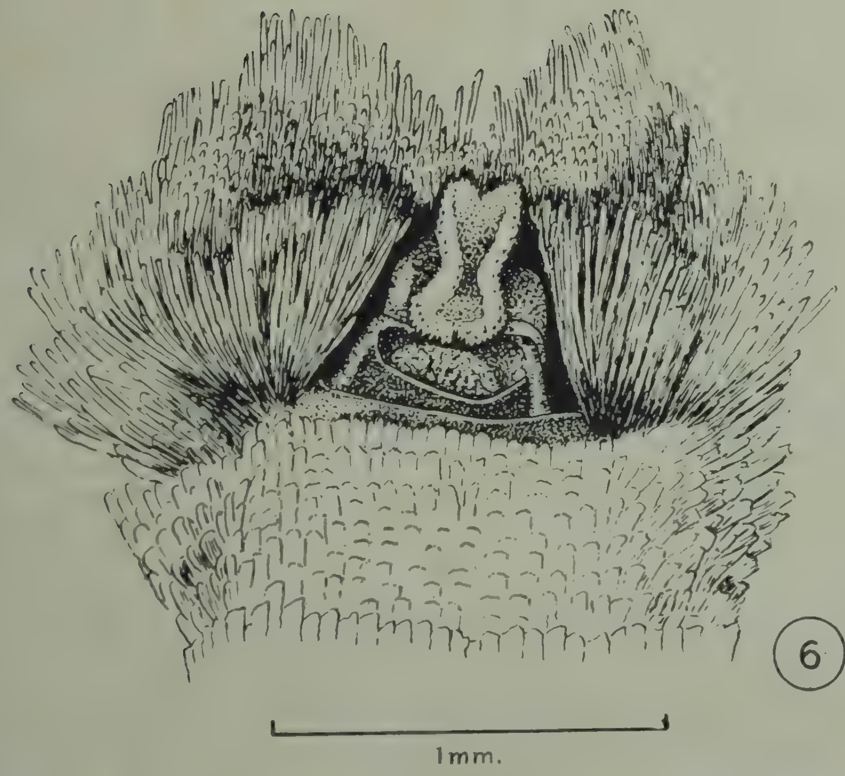

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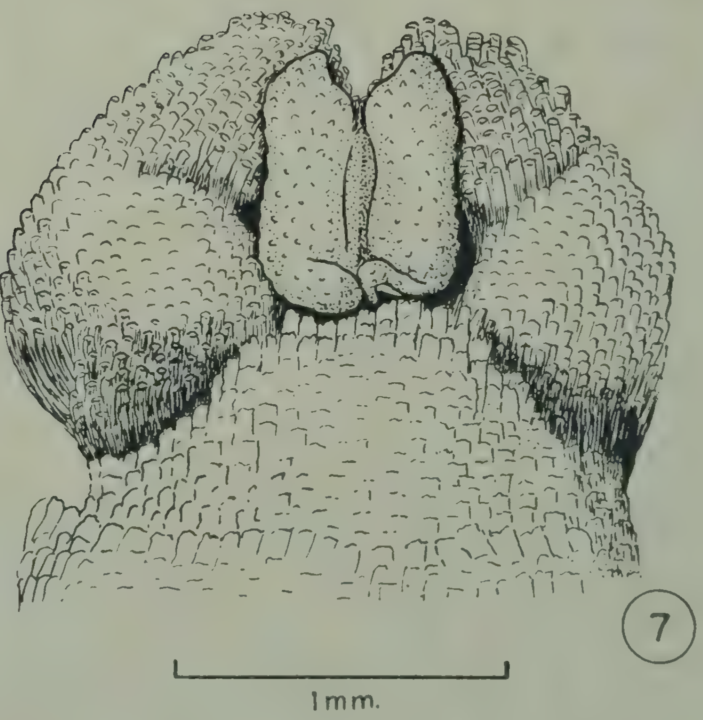

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Fig. 5. Male genitalia of *Procalyptis parooptera* (Turn.) (subfamily Archipinae).

Fig. 6. Ventral view of posterior end of abdomen of *Capua euphona* Meyr., showing "corethrogyne" scales subfamily Epitymbiinae).

Fig. 7. Ventral view of posterior end of abdomen of *Isotenes miserana* (Walk.) showing "corethrogyne" scales (subfamily Archipinae).

orifice, in the Archipinae specialization has proceeded in a different direction. The tegumen, valva and sacculus have remained lightly or moderately sclerotized, though often ornamented with long scales, the pulvinus has developed, and the transtilla has become spinose or vestigial. With the disappearance of the transtilla, its function has been assumed by the greatly developed and spinose basal processes of the valvae (Obraztsov 1954) which have often become lightly fused in the centre. In addition, the eighth abdominal sternite has developed a mensis ventralis which usually bears long scales. The limen and ostium of the female have remained relatively simple in form, but the colliculum has acquired a ventral split in the more specialized forms while a cestum and capitulum have appeared in many species.

The least specialized Australian genera include *Thrincophora* Meyr., *Isochorista* Meyr., *Cryptoptila* Meyr. and a group of species previously assigned by Meyrick to the Palearctic genus *Cnephasia* Curtis. These have a narrow uncus and large socii in the male, whilst the female signum is a tapering spine or thorn without a capitulum. In *I. panaeolana* Meyr. and *I. acrodesma* (Low.) the signum is a series of four thorns. The valvae are simple and the transtilla is densely clothed with short spines above. *Cryptoptila*, of which *Arctephora* Diak. is a synonym, has a signum which is exceptional in the subfamily. The male genitalia indicate a close relationship to *Thrincophora*, but the signum in the female is a round or ovate dentate plate. In addition a cubital pecten is present in the hindwing.

Several genera including *Acropolitis* Meyr., *Aristocosma* Meyr., *Atelodora* Meyr., *Glyphidoptera* Turn. and many species which Meyrick and Turner referred to *Capua* form a rather more specialized group. Here the uncus of the male becomes more spatulate and the socii greatly reduced, while a capitulum and a cestum are often present in the female. The female of *Capua euryochra* Turn. possesses a dense brush of "*corethrogyne*" scales similar to that found in *Capua euphona* Meyr. and its allies in the Epitymbiinae.

The most specialized genera of the Archipinae include *Homona* Walk., *Adoxophyes* Meyr., *Epiphyas* Turn., *Dichelopa* Low. and *Procalyptis* Meyr. (Fig. 5). The spatulate uncus is often very broad, the socii are reduced and the transtilla often absent. A mensis ventralis, found nowhere else in the Tortricidae except in the genera related to *Zacorisca*, is usually present. The valva sometimes has a longitudinal fold and the sacculus sometimes bears a small thorn. The tegumen and the valvae are often ornamented with very long dense scales. The colliculum is split ventrally and a cestum and capitulum are present in the females of many species.

Most of these characters are also found in *Isotenes* Meyr., the only Australian representative of a group of genera which Diakonoff (1941) separated from the Archipinae as the Zacoriscini. Here the socii have almost entirely disappeared and the valvae are rather more specialized. However, corethrogyne scales said to be characteristic of the females are also present in two Australian genera which belong elsewhere. Except for this character, Diakonoff (1952a) has shown that the genera of the Zacoriscini and the Archipinae intergrade. It seems therefore that *Isotenes* and its allies can be regarded as highly specialized genera of the Archipinae.

PHYLOGENY OF THE SUBFAMILIES

The task of arranging the five subfamilies here delineated in phylogenetic order is admittedly difficult. Perhaps the most important feature of the venation is the degree of development of the stem of M in the cell of the forewing. As the presence of M is usually regarded as a primitive character in the Lepidoptera, the Cnephasiinae, the Schoenoteninae and the Ceracinae seem to be less specialized than the remaining subfamilies. Further a gradual reduction in the socii of the male genitalia is frequently associated with increasing specialization in the valvae and an increase in the width of the uncus (see Diakonoff 1952b). Broadly these trends are correlated with a transformation in the form of the female signum from a dentate patch to a thorn, spine, hook or dagger. The more specialized form of signum is often associated with the development of a cestum and a ventral split in the colliculum.

Of the three subfamilies in which M is developed, the Cnephasiinae have the least specialized genitalia. It seems probable therefore that the remaining Tortricidae have stemmed from a cnephasiine-like stock. The Tortricinae have lost the stem of M, the uncus has been reduced and the valvae have developed a specialized brachiola. The Schoenoteninae have retained the stem of M, but the genitalia have become greatly specialized, though still maintaining the characteristic tortricid form. The stem of M has also been retained by the Ceracinae, but the uncus has become broader, with a brush beneath the apex. In the female the seventh abdominal sternite is often strongly sclerotized and the limen modified. The Archipinae probably owe their origin more directly to the Ceracinae, by the loss of the stem of M and the acquisition of many specialized characters in the genitalia of both sexes. The Epitymbiinae have also lost M and show considerable genitalic specialization of a different kind, but the retention of the dentate signum in some genera suggests a more direct relationship to the Cnephasiinae, then to any other subfamily.

REFERENCES

Diakonoff, A. 1939. The genera of Indo-Malayan and Papuan Tortricidae. *Zoöl. Meded.* 21: 111–240.
Diakonoff, A. 1941. Notes and descriptions of Microlepidoptera (I). *Treubia* 18: 395–439.
Diakonoff, A. 1952a. Records and descriptions of Microlepidoptera (5). *Zoöl. Meded.* 31: 165–178.
Diakonoff, A. 1952b–1955. Microlepidoptera of New Guinea. Part I–V. *Vehr. Akad. Wet. Amst.* 49(1): 1–167; 49(3): 1–166; 49(4): 1–164; 50(3): 1–210.
Meyrick, E. 1881. Descriptions of Australian Micro-Lepidiptera. *Proc. Linn. Soc. N. S. W.* 6: 410–536.
Meyrick, E. 1910. Revision of Australian Tortricina. *Proc. Linn. Soc. N. S. W.* 35: 139–294.
Meyrick, E. 1913. Lepidoptera Heterocera, Fam. Tortricidae. *Genera Insect.* 149: 1–81.
Obraztsov, N. S. 1954, 1955. Die Gattungen der Palaearktischen Tortricidae I. Allgemeine aufteilung der Familie und die Unterfamilien Tortricinae und Sparganothinae. *Tijdschr. Ent.* 97: 141–231; 98: 147–228.
Pierce, F. N., and J. W. Metcalfe. 1922. The genitalia of the British Tortricidae. 101 pp. Oundle, Northants.

Taxonomy of the North American Species of *Bucculatrix*: Correlation of Genitalic Structure with Food Plant Groups

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ABSTRACT

The great diversity of genitalic structure within the genus indicates a long period of evolution and the origin of the various groups at a remote period. On the basis of genitalic structure, the genus can be divided into distinct groups, which are often correlated with food-plant groups. Species feeding on amentiferous plant families, with rare exceptions, show a characteristic type of genitalia, indicating descent from a common ancestor. A small group feeding on Malvaceae is distinguished by the lobed or divided harpe and by sclerotized plates on the eighth abdominal segment of male. Only one or two species are known to feed upon several plant families. The genitalia of such species are characterized by unique and distinctive features.

The Compositae are hosts to one-half or more of all known American species. Within this group, the greatest variety and specialization of structure of genitalia are found. Shape and armature of the harpes and socii and shape of the aedeagus vary. The genitalia of females show development from a simple unspecialized to a highly specialized type. These specializations include modifications of the ostium, tufts of specialized scales on the intersegmental membrane and segment 8, sclerotized outgrowths on segment 8; and extreme modification of the ovipositor for rasping or piercing.

Caractères distinctifs de la Sous-Famille Sparganothinae (Lepidoptères: Tortricidés) et Distribution des Genres qui la composent

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RÉSUMÉ[1]

Les papillons de cette sous-famille se distinguent généralement de ceux des autres sous-familles des Tortricidés par leurs palpes labiaux assez allongés, de forme triangulaire, et s'appuyant en partie sur le front. Ils se distinguent également par la bifurcation habituelle des nervures 7 et 8 ou R_4 *et* R_5 *de l'aile antérieure, ainsi que par une combinaison de certains caractères variables tels: une touffe de longues écailles se prolongeant à l'avant sur la tête, la conformation et la vestiture du front chez le mâle, la présence d'ocelles, un repli à la base du costa de l'aile antérieure chez le mâle, la présence de pecten à la base du cubitus de l'aile postérieure et la présence de cavités sur le tergum 2 ou les terga 2 et 3 de l'abdomen. Cependant, les distinctions génériques et spécifiques les plus marquées s'observent chez les génitalia des deux sexes. L'étude des organes sexuels a permis de diviser cette sous-famille en deux tribus qui se séparent par la présence d'un gnathos divisé en deux bras, ou par son absence totale. Dans une publication prochaine sur cette sous-famille encore peu connue, l'auteur fera la révision de quelque 210 espèces dont près de la moitié seront décrites comme étant nouvelles. Ces espèces se groupent en 8 genres dont 3 sont nouveaux.*

Les genres sont répartis à travers les régions néarctique et néotropicale, avec une abondance plus marquée des espèces dans la zone tropicale des Amériques. Par ailleurs, le genre Sparganothis *Hübner est le seul à s'étendre aux régions néarctique et paléarctique, bien qu'il ne compte que trois espèces d'occurrence dans cette dernière région, dont une seule s'étend aux deux régions. Un genre nouveau et représenté par une seule espèce, ne se rencontre que dans la région orientale.*

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[1] Etant donné la mort subite du Dr. Lambert, sa publication sera achevée par le Dr. T. N. Freeman, section entomologique, Ottawa. Ont., et celle-ci paraîtra en deux parties. Nous espérons pouvoir publier la première et principale en 1959 et la seconde en 1960 comme supplément au Canadian Entomologist.

Hampson's Schoenobiinae (Lepidoptera: Pyralidae)[1]

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Hampson (1895) erected the subfamily Schoenobiinae to include a number of genera characterized by absence of a cubital pecten and absence of proboscis. Subsequently other genera were described, mainly by Hampson, Dyar, Dognin, Meyrick and Turner; Hampson added *Siga* to the group and altered the subfamily name to Siginae. Although there is a homogeneous subfamily centering on *Schoenobius*, arbitrary adherence to the original diagnostic criteria led to the inclusion with it of an unusually wide range of unrelated elements. The only rational note has been injected by Forbes (1926), who gave a better character for the Schoenobiinae proper, and noted the pyraustine affinities of *Siga* and of *Cirrhochrista*, as well as the chrysaugine position of *Bradypodicola*, a genus allied to *Cryptoses*. Börner (1932), on the basis of the few European species, correctly noted the relationship of the Schoenobiinae and Crambinae and their close affinity to the Pyraustinae and allies. If a division of the Pyralidae into smaller families proves desirable, it is likely that this large group of subfamilies will remain associated, under the old and suitable name Crambidae; at any rate, the arbitrary and artificial division adopted by Meyrick has little to recommend it.

As pointed out by Forbes, the true Schoenobiinae can be separated from the Crambinae by the presence in the former of a tubular first anal vein at the margin of the primaries. I have not yet encountered an instance where separation on this ground appears unnatural. *Leucargyra* Hmps., described as a crambine, goes on the anal vein character into Schoenobiinae, where its habitus and genitalic structure also would place it. The following additional nominal genera of which I have sufficient knowledge should remain in Schoenobiinae: *Acentropus* Curt., *Apurima* Wlk., *Brihaspa* Moore, *Catagela* Wlk., *Crambostenia* Swinh., *Leechia* South, *Microschoenis* Meyr., *Panalipa* Moore, *Rupela* Wlk., *Schoenobius* Dup., *Scirophaga* Tr., *Schoenoploca* Meyr., *Alloperissa* Meyr., *Limnopsares* Meyr., *Patissa* Moore, *Leptosteges* Warr., *Tipanaea* Wlk., *Argyrostola* Hmps., *Topeutis* Hbn., *Leucoides* Hmps., *Donacaula* Meyr., *Niphopyralis* Hmps., *Neoschoenobia* Hmps. and *Eurycraspeda* South.

The remaining genera belong to the most diverse groups of Pyralidae, s. l. *Siga* Hbn., as noted by Forbes, is a pyraustine; it is very closely related to the African genus *Eporidia* Wlk. (=*Glaucoda* Karsch), erroneously placed by Ghesquière in the Nymphulinae. *Cirrhochrista* Led. is also pyraustine, as Forbes correctly guessed. *Obtusipalpis* Hmps. is very close to *Cirrhochrista*. These two genera are related in a general way to *Polygrammodes* Gn. *Loxostegopsis* Dyar is another genus correctly placed in Pyraustinae by Forbes. It is closely related to *Metasia* and has no close relationship to the Nymphulinae or Scopariinae. I have not been able to examine *Loxmaionia* Schs. structurally, but its habitus leaves little doubt that it is a pyraustine, perhaps related to *Azochis* Wlk. *Micraeschus* Wlk. (=*Acropentias* Meyr.) is an unusual genus that probably is a fifth representative of the Pyraustinae. *Nymphulodes* Dyar has typical nymphuline genitalia and habitus, and should be placed in that subfamily. *Chalcoëlopsis* Dyar is a synonym of *Cryptocosma* Led. It is neither a schoenobiine nor a crambine. The habitus and the presence of raised scales on the disc of the hind wing might suggest that it is a glaphyriine, but the genitalia have a well-developed gnathos and seem to indicate a nymphuline position. *Aeglotis* Ams. is an odontiine (= titaniine), as shown by Amsel's figure of the genitalia. *Zaboba* Dyar and *Cryptoses* Dyar are unrelated Chrysauginae. The former is close to the North American *Acallis mitchelli* Dyar; the latter is a sloth moth related to *Bradypodicola* Spul. The genera *Anaeglis* Led. and *Xenophasma* Dgn. have been transferred to the Epipaschiinae; this appears to be the best disposition for *Schacontia* Dyar, too. The three genera are unrelated. *Amestria* Rag. and *Macrotheca* Rag. have already been separated as the Macrothecinae. This subfamily appears to be correctly located close to the Galleriinae.

The following discrete groups should be regarded as of uncertain placement for the present:—(1) *Banepa* Moore, to which *Pyralopsis peruviensis* Dgn. (=*Neobanepa aglossodes* Hmps.) (new synonymy) may not be really related; (2) *Micrelephas* Dgn., which is superficially reminiscent of a crambine or ancylolomiine; (3) *Eudorina* Snell. (=*Syncrotaula* Meyr.), to which *Haploscopa* Meyr. is immediately related; and (4) *Styphlolepis* Hmps. These groups are structurally well characterized, and with a better knowledge of the family as a whole they will fall into their places.

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[2] Senior Entomologist.

Another discrete group is constituted by *Midila* Wlk. (=*Singamia* Msch., =*Tetraphana* Rag.), together with the allied genera *Cacographis* Led., *Gonothyris* Hmps., *Dismidila* Dyar and *Hositea* Dyar. These are pyralid in wing venation and in the scaled tongue, but, apart from their most unusual habitus, they differ strikingly from other Pyralidae in having the tympanic bullae rudimentary and indeed hardly distinguishable. These organs do not show up distinctly in caustic-treated specimens, but they are visible in dry dissection as a pair of slits on the antero-ventral surface of the abdomen, facing the hind coxae. There is no trace of a "tablier" connecting the thorax and abdomen. This condition differs from that of the Thyrididae and Hyblaeidae, in which there is no sign of abdominal tympanal organs, even in dry dissection. Also the external characters are distinctly pyralid. However, I have no hesitation in separating the *Midila* group as a distinct subfamily, which I call Midilinae, new subfamily, type genus *Midila* Walker.

A number of genera are not known to me from specimens, or at least from material suitable for dissection, and are not obviously enough characterized to make possible a useful guess as to their positions. Some are probably true Schoenobiinae, others will add to the already remarkable list of groups mistakenly placed in the subfamily. A list of the unstudied genera follows: *Auchmophora* Turn., *Pogonoptera* Turn., *Monodonta* Kenr., *Exodesis* Hmps., *Gonopalpia* Hmps., *Endotrichodes* Hmps. *Dolichobela* Turn., *Cosmophila* Meyr. [=*Niphadaza* Butl]., *Drepanodia* Rag., *Idneodes* Rag., *Callasopia* Msch., *Platytesis* Hmps., *Paracentristis* Meyr., *Stenocalama* Hmps., *Thyridopsis* Ams., *Thyridiphora* Warr., and *Cyclocausta* Warr.

REFERENCES

Börner, C. 1932. Die Tierwelt Deutschlands. Schmetterlinge oder Lepidoptera. III. Nachtfalter (Heterocera): Microlepidoptera. Jena.

Forbes, W. T. M. 1926. The relationships of some aberrant pyralids (Lep.). *J. New York Ent. Soc.* 26: 331–340.

Hampson, G. F. 1895. On the classification of the Schoenobiinae and Crambinae, two subfamilies of moths of the family Pyralidae. *Proc. Zool. Soc. Lond.* 1895: 897–974.

Die Tegula der Lepidoptera, ihre Funktion und taxonomische Verwertbarkeit

Von Erich M. Hering
Berlin–Dahlem, Germany

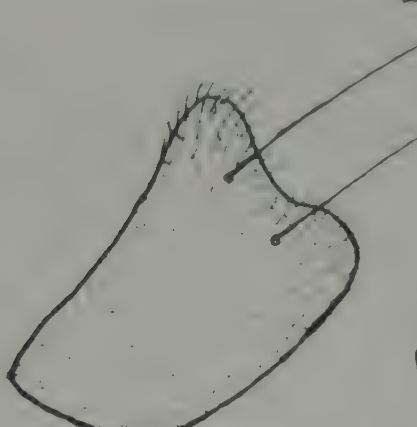
Als Tegulae bezeichnet man zwei seitliche Sklerite des Mesotergums der Insekten, die schuppenartig die Basis des Vorderrandes der Vorderflügel überdecken. Bei den Lepidoptera sind diese Gebilde am stärksten entwickelt und differenziert; in schwächerer Ausbildung werden sie bei Rhynchota, Diptera, Hymenoptera und Trichoptera angetroffen. Ihre erstmalige (und heutige) wissenschaftliche Bezeichnung prägten Kirby & Spence (1826), die sie scharf von den Patagia, Ausstülpungen des Prothorax, unterschieden (mit denen sie doch in der Folgezeit gelegentlich verwechselt wurden). Weitere Bezeichnungen für sie sind Epaulets (Comstock, Townsend), Paraptera (McLeay), Pterygodes (Latreille), Pterygoide (C. H. French), Scapulae (W. F. Kirby). Bei höheren Diptera findet man distal von der Tegula ein weiteres Skelettstück, das Subepaulet (Townsend), das aber wahrscheinlich von der Costalader des Flügels abgegliedert wurde (Fig. 2); bei den Lepidoptera tritt es niemals auf. Bei primitiven Diptera ist die Tegula nur ein kleines, behaartes Kissen, das aber bereits einige längere Borsten erkennen lässt (Fig. 1). Bei *Bombus* (Hymenoptera) ist die Tegula gross (Fig. 3) und so mit dem Flügel gekoppelt, dass beim Heben der Tegula beim frisch getöteten Tier der Vorderflügel sich nach vorn bewegt. Die Tegulae der Lepidoptera sind in Bau und Anheftungsweise mit denen der genannten Ordnungen nicht ohne weiteres vergleichbar. Ihre morphologische Sonderstellung innerhalb der Insekten hat schon Snodgrass (1909) betont: "In the Lepidoptera the tegula is so large that it is supported by a special plate of the mesonotum, which in turn is supported by a large tegular arm from the base of the pleural wing process". Beim Vergleich der Ausbildung dieses Sklerites in der mutmasslichen engeren Ahnenreihe der Schmetterlinge stellt man bei *Panorpa* (Panorpatae) eine sehr kleine, gleichmässig kurz beborstete Schuppe fest, die noch in ganzer Breite dem Thorax ansitzt und der Flügelbasis wohl kaum einen Schutz gewähren, auch als Flügel-Gelenkstück nicht fungieren kann. Bei *Phryganea* (Trichoptera) ist das Sklerit aber bereits in einer Form entwickelt, wie sie bei manchen Rhopalocera ausgebildet ist, etwa wie bei *Acraea* (Fig. 36). Der Hautschlauch, der es mit dem Thorax verbindet, besitzt aber einen viel grösseren Durchmesser, seine Anheftung liegt ganz auf der Ventralkante, etwa wie bei *Danaus*. Die konvexe Aussenseite der Tegula ist mit Borsten besetzt. Bemerkenswert ist dass an der ventralwärts gerichteten Ecke des Sklerites sich eine ganz schwach knopfartige Vorwölbung findet, deren Borsten andersartige Form, Farbe und dichtere Stellung zeigen. Diese Ecke zeigt bereits die Potenz zur Ausbildung des ventralen Fortsatzes, der dann bei den Lepidoptera gefunden wird. Die dem Flügelrand zugewendete Innenseite gleicht in ihrer Glätte und fehlendem Borstenbesatz einer Gelenkpfanne; in sie ragt eine etwa kugelige Abgliederung der Costalader als Gelenkkopf. Die Tegula von *Phryganidia* ist unzweifelhaft funktionell ein Analogon zu den Axillaria.

BAU DER TEGULA

Von den primitivsten Lepidoptera, den Micropterygidae, bis zu den höchststehenden Rhopalocera zeigt die Tegula eine gewisse Uniformität. Sie besteht aus einem im Umriss etwa dreieckigen Zentralkörper (C, Figs. 49, 50), dessen Scheitel auf dem Vorderflügel-Vorderrand liegt. An der der Flügelbasis zugewendeten Innenfläche ist er durch eine häutige Röhre mit dem Mesothorax verbunden. Ihre Entwicklung kann man sich so vorstellen, dass das ursprünglich am Mesotergum liegende Sklerit distalwärts in Richtung der Flügelspitze sich verschob; die das Sklerit umgebende Bindehaut folgte dieser Verschiebung, wobei sie sich röhrenförmig verengte. Sie ist niemals stärker sklerotisiert, daher lässt sich die Tegula meist leicht vom Thorax ablösen. Dabei entsteht an der Ablösungsstelle an der Innenseite des Sklerites ein Loch (L, Figs. 49, 50), den Rand der Anheftungsstelle des Bindehautschlauches bezeichnend. Die Lage dieses Loches—am Ventralrand oder mehr im Zentrum—ist taxonomisch wichtig. Die Weichheit der häutigen Röhre ermöglicht die Beweglichkeit der Tegula. Die der Flügel-Basis zugewendete konkave Innenseite des Zentralkörpers ist immer unbeschuppt, glänzend-glatt, wie poliert, erscheint wie eine Gelenkpfanne und wird wohl eine analoge Funktion besitzen, wobei die Basis der starken und stark beanspruchten Costalader als Gelenkkopf wirksam sein kann. Bei hochstehenden

Rhopalocera lässt sich eine Entwicklungs-Tendenz verfolgen, die Innenseite der Tegula immer mehr zu verdünnen; bei manchen Satyrinae (Figs. 45, 46) ist sie mit Ausnahme einer schmalen, stärker sklerotisierten Randzone ganz häutig geworden. Die konvexe

1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Tipulid. Dipt.
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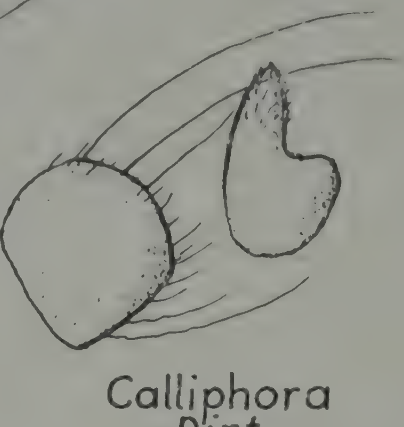
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Dipt.

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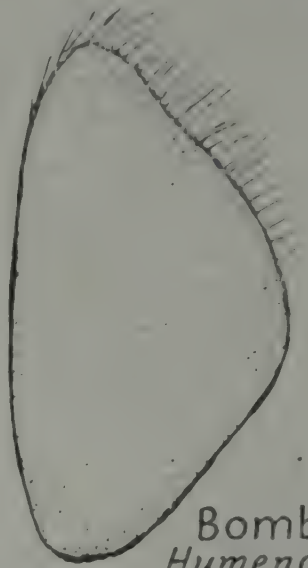
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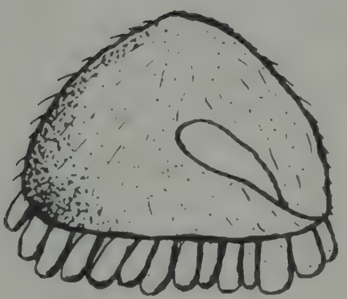
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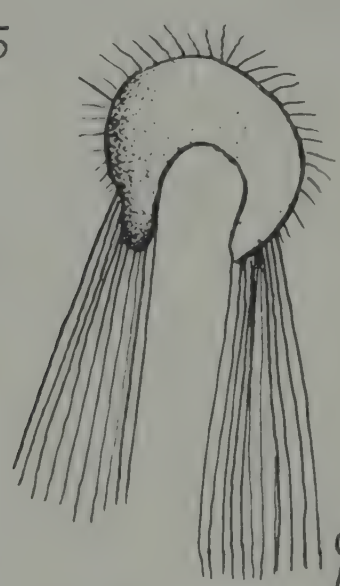
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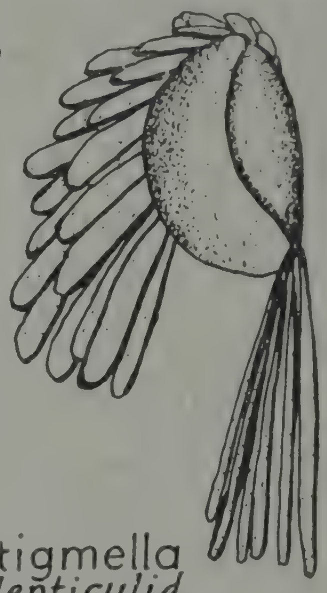
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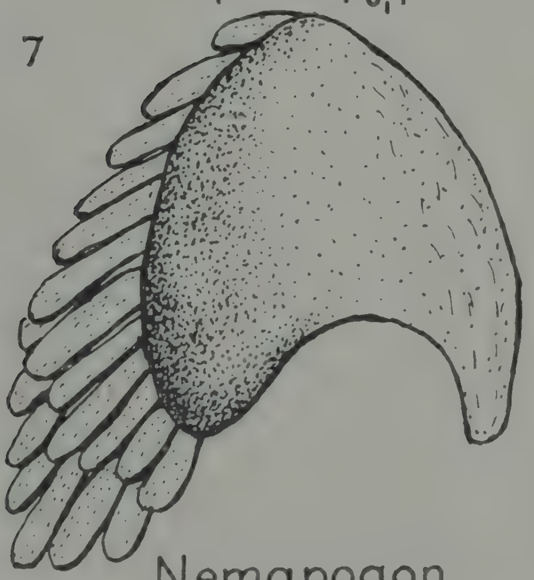
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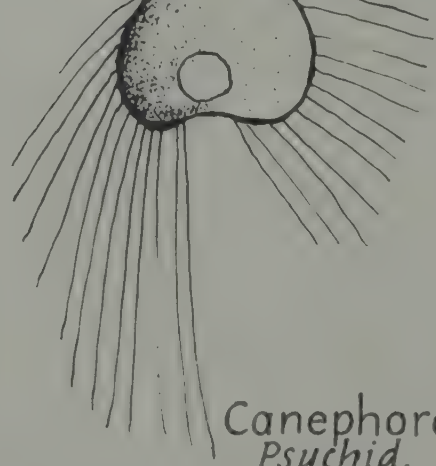
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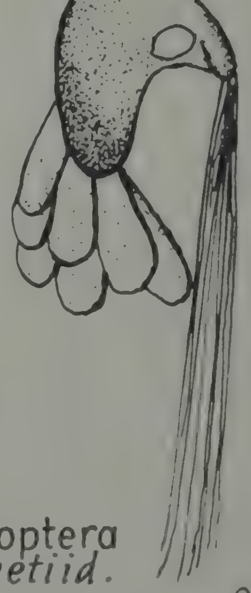
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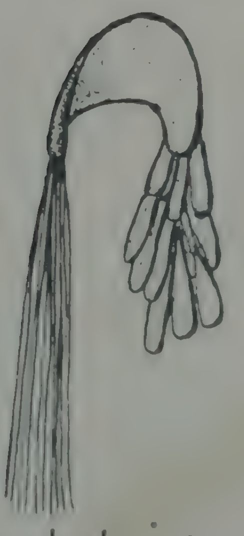
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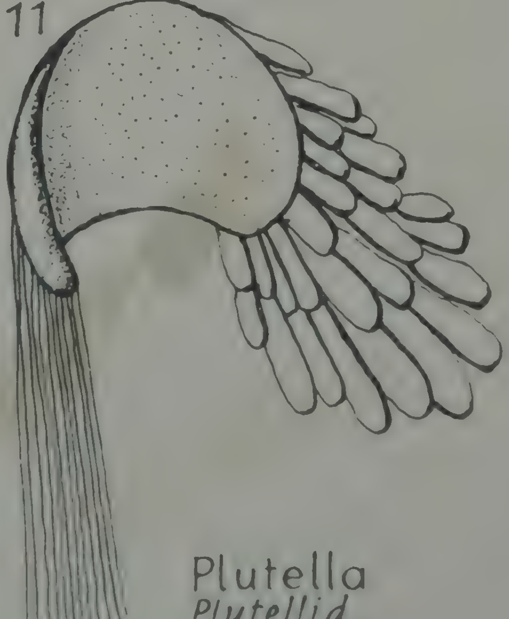
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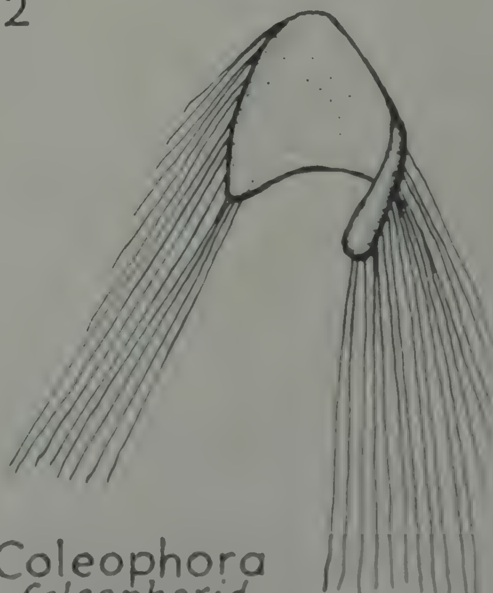
12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Coleophorid.
0,1

Aussenseite des Sklerites ist immer mit Schuppen besetzt, die meist denen der Thoraxbekleidung gleichen, also entweder breit und platt oder haarförmig sind; zuweilen finden sich Schuppen von beiderlei Gestalt. Die Schuppenfärbung entspricht im dorsal liegenden Teile der des Thorax, im ventralen der der Vorderflügel-Unterseite.

Der Zentralkörper ist vielfach an den dorsal und ventral liegenden Ecken verlängert und verschmälert, fortsatzartig ausgezogen. Diese Fortsätze sollen hier als der dorsale (d, Figs. 49, 50) und der ventrale (v) bezeichnet werden. Der dorsale Fortsatz liegt dem Thorax an, er ist häufig besonders lang und schmal, dann länger als der Ventral-Fortsatz. Dieser letzte liegt an der Unterseite der Vorderflügel-Basis an; er wird häufig bei den verschiedensten Familien auch dann gefunden, wenn ein Dorsalfortsatz nicht vorhanden ist. Das Fehlen von Fortsätzen wird nicht nur bei den primitiven *Micropteryx* (Fig. 4), sondern auch sonst an verschiedenen Stellen des Systems beobachtet, so etwa innerhalb der Macrofrenatae bei *Ratarda* (Fig. 27), bei Rhopalocera bei *Oeneis* (Fig. 46). Geschlechts-Verschiedenheiten werden, wo solche ausgeprägt sind, besonders am Dorsalfortsatz festgestellt; dieser ist beim ♂ von *Casuaria* schlanker und länger; bei *Epicopeia* ist er beim ♀ verlängert, während gleichzeitig der Ventralfortsatz kürzer ist; bei *Callidula* sind beide beim ♀ breiter. Die Beschuppung der Zentralkörper-Aussenseite geht auch auf die der Fortsätze über und verlängert sich meist über deren Ende hinaus in auffallende Schuppenbüsche, die von besonderer Bedeutung für die Taxonomie und wohl auch für die Funktion sind. Dorsaler und ventraler Schuppenbusch sind vielfach in der Schuppengestalt sehr verschieden. Während der dorsale Schuppenbusch sich wie sein Fortsatz dem Thorax anlegt, reicht der ventrale vielfach weit nach hinten und überdeckt von unten her die Basis des Frenulums bei den Frenaten, die eine Haftborste besitzen, oder das vorgezogene Humeralfeld der Hinterflügel bei Frenaten, denen diese primär fehlt (Saturniidae, Lasiocampidae etc.) und den Rhopalocera. Bei den höheren Rhopalocera ist eine Entwicklungs-Tendenz zu beobachten, die Fortsätze rückzubilden. Das geschieht entweder durch ihre Einbeziehung in den Zentralkörper oder durch verminderte Sklerotisierung (*Pieris*, Fig. 35).

Weber (1926, 1933) fand einen in die Tegula führenden Musculus tegulae bei *Vespa crabro* L. (Hymenoptera), durch den er die Bewegbarkeit der Tegula vermittelt sieht. An untersuchten Lepidoptera konnte dieser Muskel nicht gefunden werden. H. J. Hannemann (mündlich) fand an seiner Stelle einen kräftigen Nerv, der ins Innere der Tegula führt und sich ausschliesslich an der dem Flügel-Vorderrand anliegenden Ventralseite fein verästelt. Bei *Nemapogon* (Tineidae) wurden nach der Entschuppung auf dem Ventralfortsatz winzige Börstchen gefunden, die vielleicht als Sinnesorgane anzusprechen sind.

FUNKTION DER TEGULAE

Herkömmlicherweise ist die Tegula immer nur als ein Gebilde angesprochen worden, das als Schutz der weichen Basis der Vorderflügel gegen Verletzung und Verschmutzung wirksam ist. Es ist kaum anzunehmen, dass man hierin ihre ursprüngliche Funktion zu sehen hat. Man sieht bei primitiven Diptera ganz deutlich, dass sie dafür zu kurz ist. Zudem besteht eine erhöhte Gefährdung der von ihr bedeckten Teile der Flügel-Basis nicht. Es scheint, als ob dieses merkwürdige Sklerit eine Anzahl verschiedener Funktionen ausüben kann, von denen die eine oder die andere je nach der in Frage kommenden Gattung allein wirksam sein oder doch wenigstens dominieren kann. Als möglich können die folgenden Funktionen angesehen werden:

1. Die Tegula kann als Ersatz für ein Flügel-Gelenkstück wirksam sein. Während die Flügeladern *sc* bis *an* den Axillaria (Pteralia) 1–3 gelenkig verbunden sind, fehlt der oft starken und für den Flug besonders wichtigen Costalader bei den Familien, deren Vorderflügel-Vorderrand an der Basis stark vorgezogen ist (so bei gewissen Macrofrenatae und vielen Rhopalocera), ein solches Axillare. Es ist anzunehmen, dass in solchen Fällen die Tegula für die Costalader eine analoge Bedeutung hat wie die Axillaria für die übrigen Flügeladern. Für eine solche Wirksamkeit spricht auch die grosse Beweglichkeit dieses Sklerites.

← Figs. 1–12. Tegula. 1, *Flabellifera elegans* Mg. (Dipt. Tipulidae); 2, *Calliphora vomitoria* L. (Dipt. Calliphoridae) (mit "Subepaulet"); 3, *Bombus* spec. (Hymen. Apidae); 4, *Micropteryx calthella* L.; 5, *Cibyra sylvina* L.; 6, *Stigmella betulicola* Stt.; 7, *Nemapogon granellus* L.; 8, *Canephora unicolor* Hufn.; 9, *Leucoptera spartifoliella* Hb.; 10, *Bucculatrix crataegi* Z.; 11, *Plutella maculipennis* Curt.; 12, *Coleophora unipunctella* Z.

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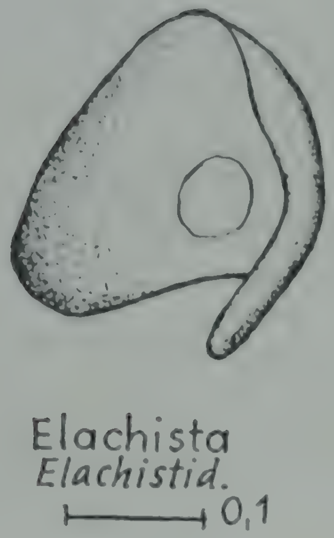
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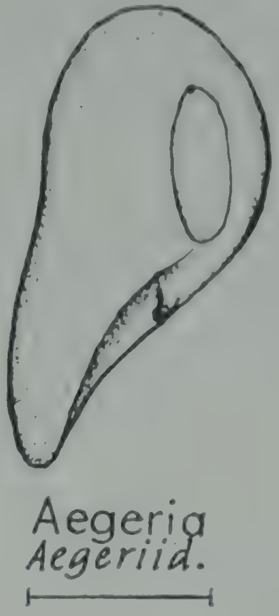
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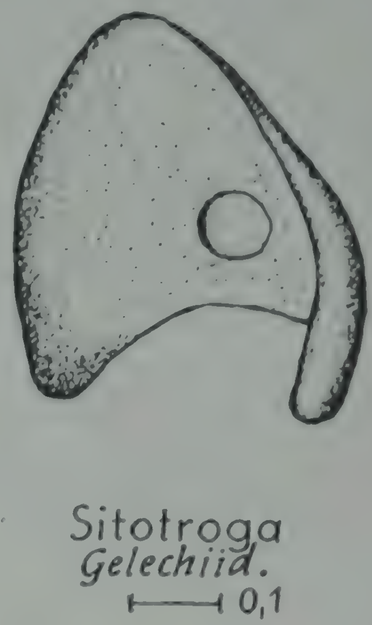
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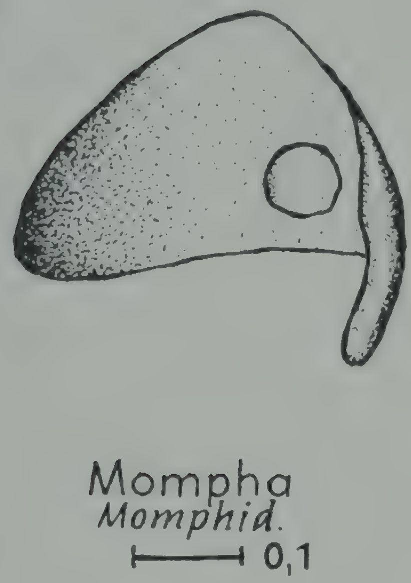
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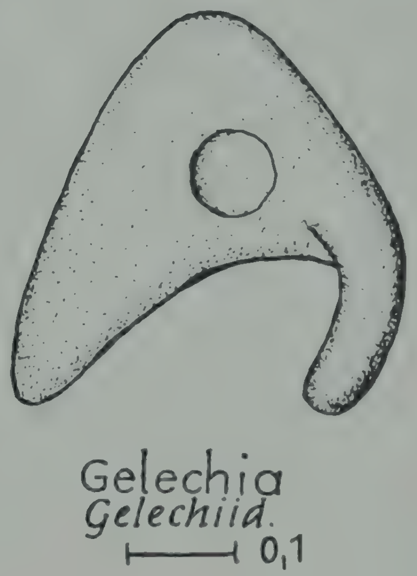
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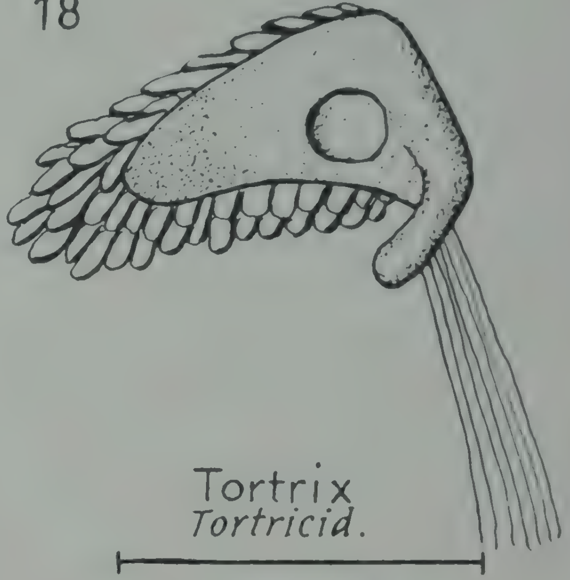
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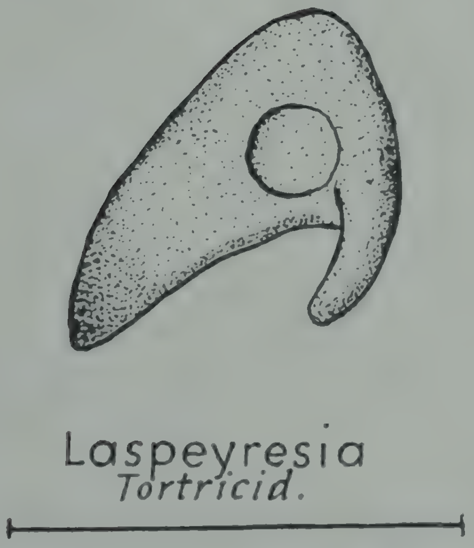
19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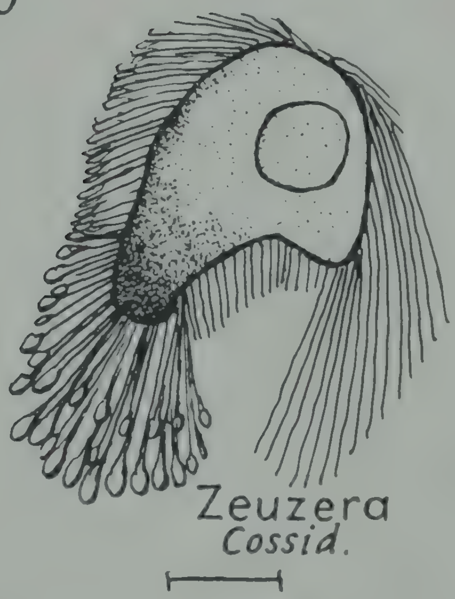
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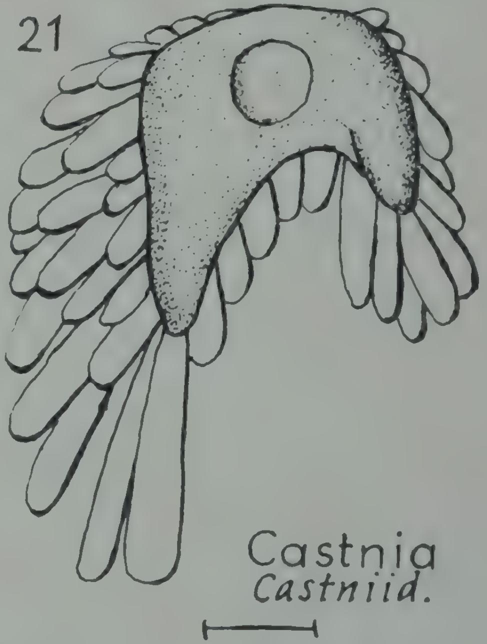
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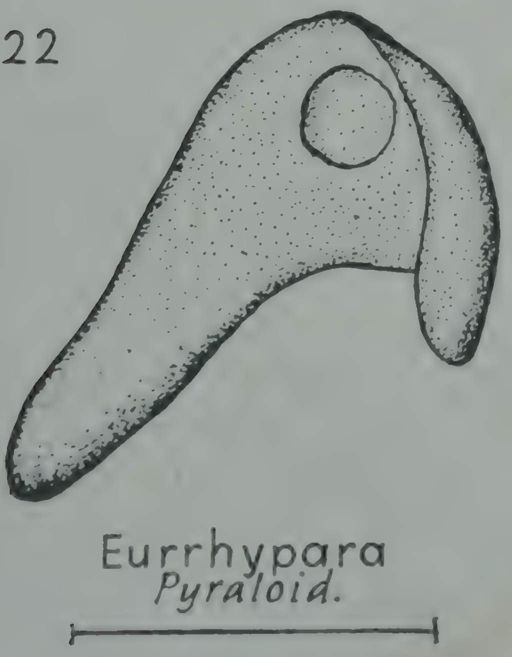
Eurrhypara
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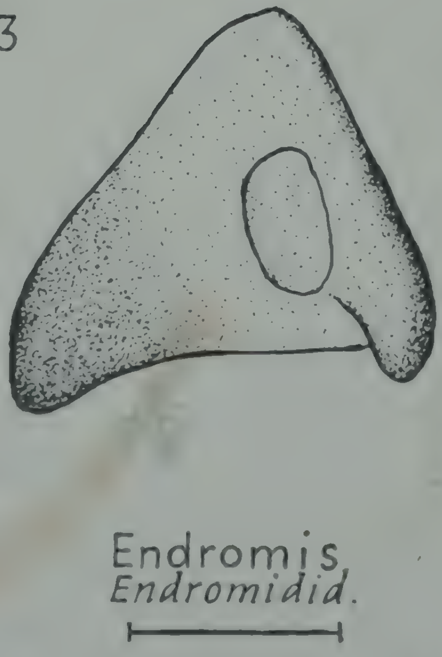
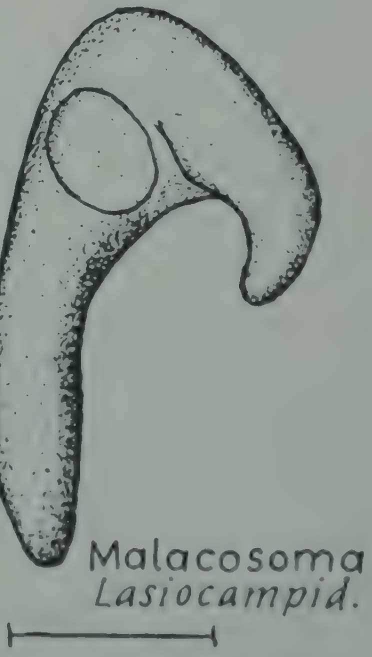
23


Endromis
Endromidid.

24


Malacosoma
Lasiocampid.

Figs. 13–24. Tegula. 13, *Elachista nigrella* Hw.; 14, *Aegeria apiformis* L.; 15, *Sitotroga cerealella* Ol.; 16, *Mompha propinquella* Stt.; 17, *Gelechia* (s.l.) *peliella* Tr.; 18, *Tortrix viridana* L.; 19, *Laspeyresia pomonella* L.; 20, *Zeuzera pyrina* L.; 21, *Castnia (Athis) orestes* Wlk.; 22, *Eurrhypara urticata* L.; 23, *Endromis versicolora* L.; 24, *Malacosoma neustria* L.

2. Bei den Frenaten ist wohl die Hauptfunktion der Tegula eine Verstärkung der Flügel-Koppelung. Sie wirkt dabei etwa wie ein Hebel, dessen oft längerer dorsaler Arm am Thorax Widerstand findet, während der lange ventrale Schuppenbusch die Basis des Frenulums gegen die Unterseite des Vorderflügels presst, so das Herausgleiten der Haftborste aus dem Retinakulum erschwerend. Man wird die Wirkung eines Schuppenbusches in diesem Sinne nicht unterschätzen, wenn man sich an das nur aus wenigen Schuppen auf der Cubitalader bestehende Retinakulum des ♀ der meisten Frenaten erinnert. Analog dazu wird bei Lepidoptera, denen das Frenulum fehlt, der vorgezogene Humeralteil des Hinterflügels gegen den Vorderflügel gedrückt. Bei den Homoneura, deren Vorderflügel-Wurzel besonders stark verschmälert ist, kommt eine solche Wirksamkeit nicht in Frage. Bei den Microfrenatae, bei denen ventraler Fortsatz und Schuppenbusch besonders deutlich ausgeprägt sind und nur selten fehlen, scheint diese Verstärkung der Frenulum-Fixierung die Hauptfunktion darzustellen.

3. Es lässt sich auch vermuten, dass die Tegula dem Falter wichtige Sinnesempfindungen über die Flügelstellung, den Luftwiderstand etc. vermitteln kann. Nur so lässt es sich erklären, dass der von Hannemann gefundene Nerv, der in die Tegula hineinführt, sich gerade dort fein verästelt, wo die Tegula den innigsten Kontakt mit dem Flügel-Vorderrand hat. In diesem Zusammenhange sei auch an die als Sinnesbörstchen angesehenen winzigen Härchen erinnert, die bei *Nemapogon* gefunden wurden und sicherlich auch anderwärts vorkommen werden.

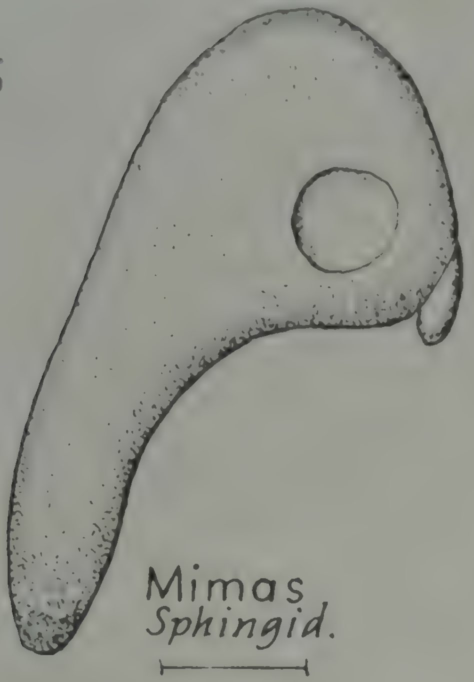
4. Die Tegula wird infolge ihrer bei Lepidopteren oft sehr beträchtlichen Grösse einen gewissen Schutz weichhäutiger Teile der Flügel-Basis bewirken können, dies aber sicherlich nur in einer Nebenfunktion. Dass im Zusammenhang mit dieser die vielfältigen Differenzierungen der Fortsätze und Schuppenbüsche erfolgt sind, ist ganz unwahrscheinlich, da diese nicht mehr der eigentlichen Flügelwurzel zugutekommen.

TAXONOMISCHE VERWENDBARKEIT DER TEGULA

Trotz der recht beachtlichen Verschiedenheiten im Bau der Tegula der Lepidoptera sind bisher kaum Versuche unternommen worden festzustellen, wieweit diese Differenzen zur Unterscheidung von Arten, Gattungen oder Familien gebraucht werden können. Einzig Jordan (1928) berichtet nach umfangreichen Untersuchungen über die Verwendbarkeit zur Trennung der Rhopalocera von den Heterocera (einschliesslich der Hesperiidae): nach ihm liegt die Anheftungsstelle des Bindehautschlauches (und damit das beim Abtrennen der Tegula entstehende Loch an ihrer Innenseite) bei den Rhopalocera stets am Unterrande der Tegula, bei den Heterocera vom Unterrande entfernt, mehr oder weniger zentral. Die Feststellungen von Jordan haben aber keine weiteren Veröffentlichungen über die Brauchbarkeit der Tegulae für die Taxonomie zur Folge gehabt. Die nachfolgende Darstellung soll eine Anregung geben, diesen eigenartigen Gebilden die Aufmerksamkeit der Taxonomen zuzuwenden, da ihre Bauverschiedenheiten es wahrscheinlich machen, dass man mit ihrer Hilfe wenigstens Arten, wenn nicht auch höhere Kategorien wird unterscheiden können. Es soll aber betont werden, dass bei der bildlichen Wiedergabe nur Beispiele, keine Typen der Gattungen dargestellt werden; der Gattungs-Charakter in der Tegula-Gestaltung kann erst dann begründet werden, wenn von den in Frage kommenden Genera wenn nicht alle, so doch der grösste Teil der Arten untersucht sein wird. Sinngemäss gilt das noch mehr für die Erarbeitung der tegularen Familien-Kennzeichnung durch Untersuchung recht vieler, namentlich der etwas abseits stehenden Genera.

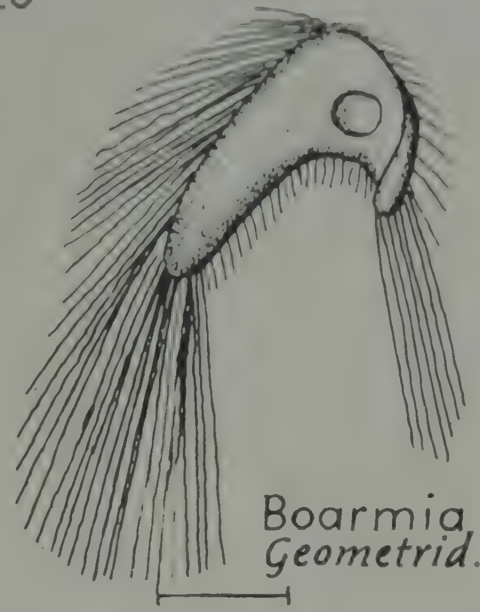
Bei der primitivsten Familie der Lepidoptera, den Micropterygidae, zeigt *Micropteryx* (Fig. 4) eine noch schuppenförmige Ausbildung der Tegula, die sich fast ringförmig um die Vorderflügel-Basis legt. Die Entwicklung der Forsätze erscheint bereits angedeutet, namentlich erinnert der Ventralfortsatz schon an die Ausbildung, die er bei manchen Frenaten und Rhopaloceren erhalten hat. Ihm fehlt aber vollständig jedes abgesetzte Schuppen-oder Haarbüschel, wie es bei den höheren Microlepidoptera ausgeprägt ist. Damit scheint jede Verstärkung der Flügel-Koppelung ausgeschlossen, zumal ihr auch die starke Verschmälerung der Vorderflügel-Basis entgegensteht, die für die Homoneura kennzeichnend ist.-Bei *Cibyra* (Hepiol.) (Fig. 5) sind die beiden Fortsätze bereits angedeutet; jeder ist mit langen Schuppenhaaren bekleidet; eine Unterstützung der Flügelkoppelung durch sie ist aber auch hier unwahrscheinlich.—*Nemapogon* (Tineid.) (Fig. 7) besitzt bereits den langen Haarbusch

25



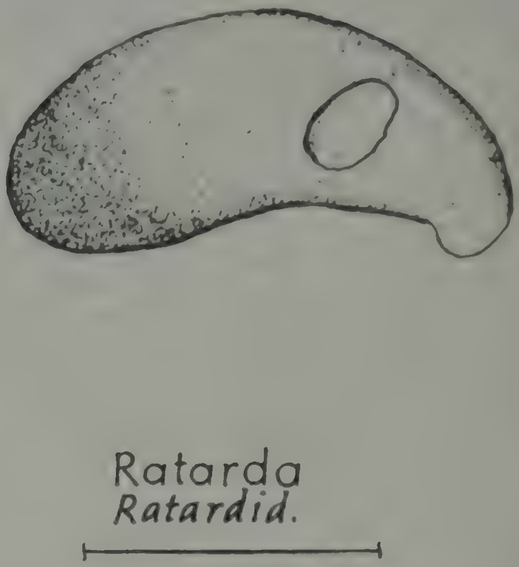
Mimas
Sphingid.

26



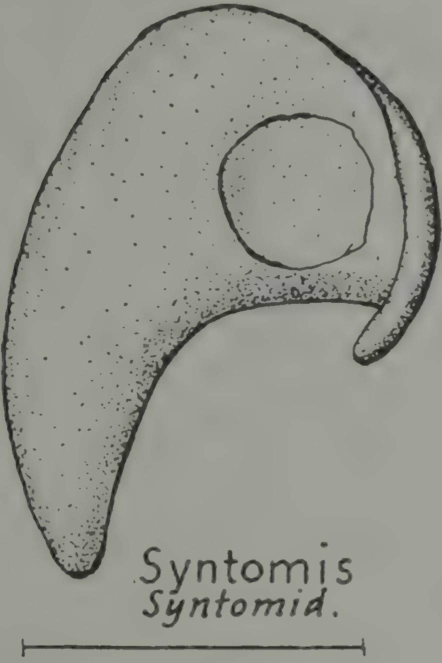
Boarmia
Geometrid.

27



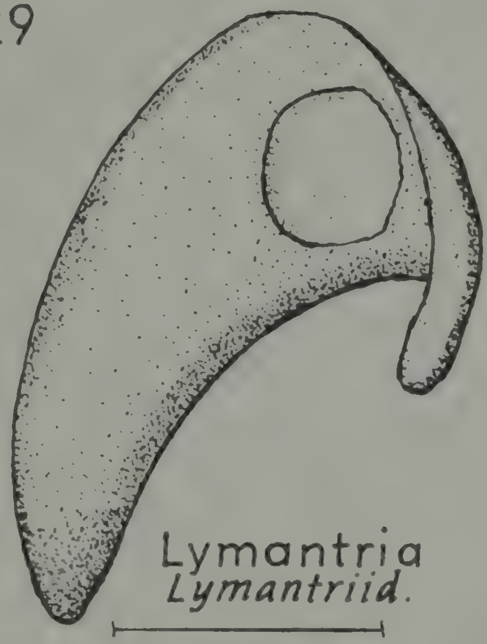
Ratarda
Ratardid.

28



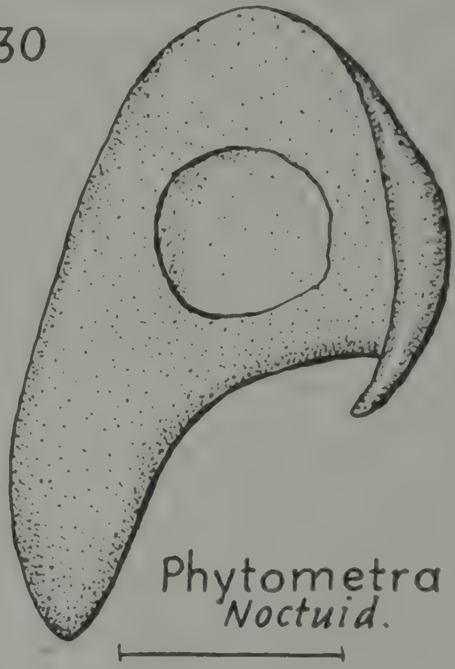
Syntomis
Syntomid.

29



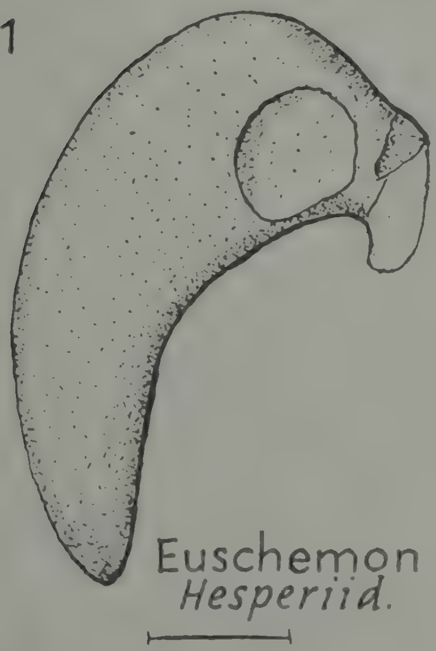
Lymantria
Lymantriid.

30



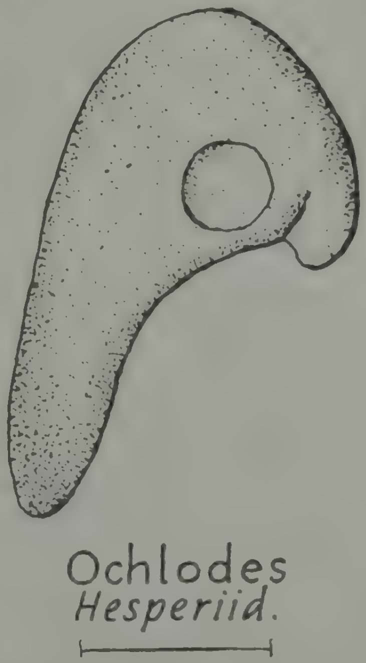
Phytometra
Noctuid.

31



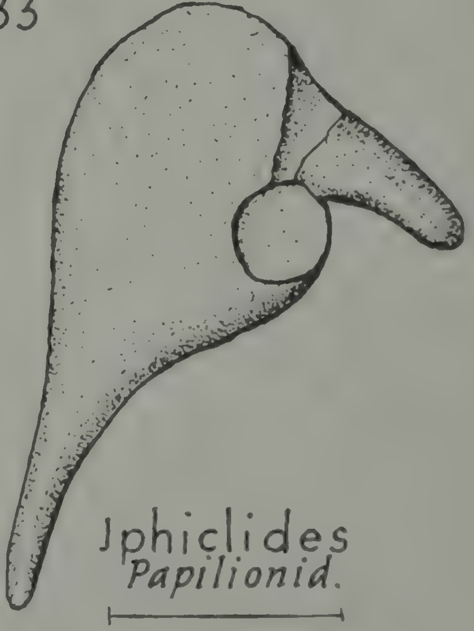
Euschemon
Hesperiid.

32



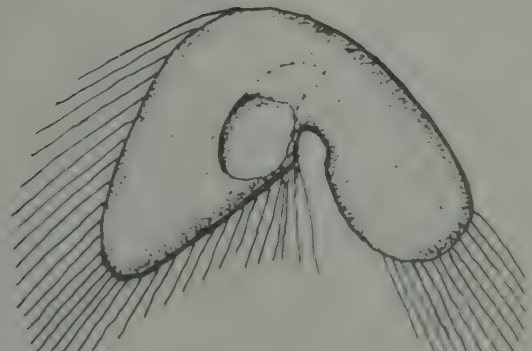
Ochlodes
Hesperiid.

33



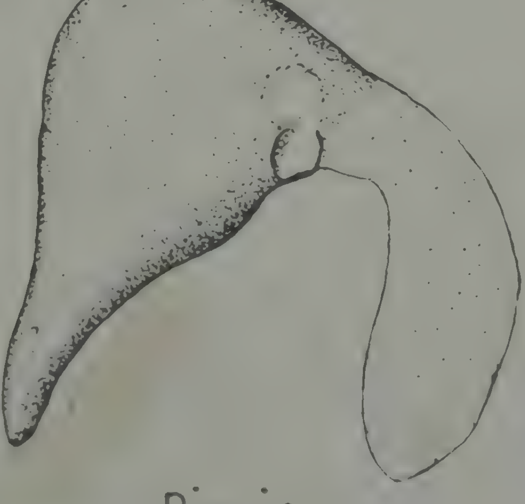
Jphiclides
Papilionid.

34



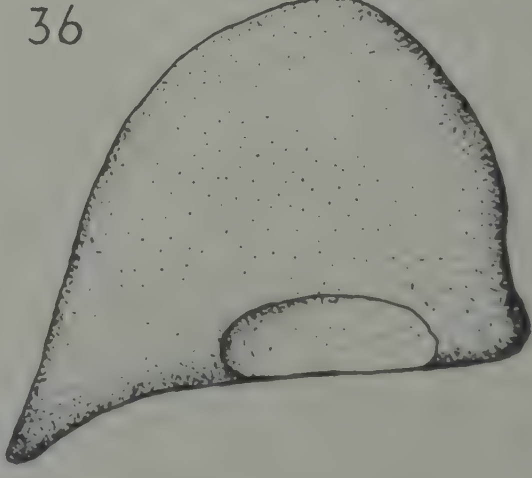
Parnassius
Papilionid.

35



Pieris
Pierid.

36



Acraea
Nymphalid.

des Ventral-Fortsatzes; er wurde hier entfernt, um das Vorhandensein der feinen als Sinnesbörstchen angesprochenen Härchen zu verdeutlichen Wie bei den folgenden drückt auch hier der lange Schuppenbusch gegen die Basis des Frenulums und verstärkt die Flügel-Koppelung. —Bei *Stigmella* (Nepticulid.) (Fig. 6) sind keine deutlichen Fortsatzbildungen, dagegen sehr ausgeprägte Schuppenbüsche zu sehen; der dorsale besteht aus den breiten Schuppen, wie sie den Thorax bekleiden, der ventrale trägt längere, stark verschmälerte, fast haarförmige.— Bei *Leucoptera* und *Bucculatrix* (Lyonet.) (Figs. 9, 10) sind bereits die Fortsätze deutlich; der ventrale trägt ausgesprochene, lange Haarschuppen.—*Canephora* (Psych.) (Fig. 8) zeigt keine Fortsätze und keine abgehobenen Schuppenbüsche; beide bestehen aus Schuppenhaaren, die sich nur durch etwas grössere Länge von der sonstigen Tegula-Bekleidung abheben.— Bei *Ypsolophus* und *Plutella* (Plutell.) (Fig. 11) sind die beiden Büsche zwar in der Schuppenform verschieden, aber der ventrale ist relativ kurz, wohl im Zusammenhang damit, dass an der Unterseite der Vorderflügelwurzel ein distalwärts gerichtetes Schuppenbüschel am Vorderrand entspringt, das das Frenulum an den Vorderflügel andrückt und so die vermutete Funktion des Tegula-Busches für die Flügelkoppelung übernimmt.—Bei *Coleophora*(Coleophor.) (Fig. 12) ist die Tegula besonders hoch, beide Ecken mit Haarbüschen bekleidet, der Ventralfortsatz deutlich abgesetzt.—Die Tegulaform der Gracillariidae und Elachistidae (*Elachista*, Fig. 13) ist ähnlich, die Dorsalecke trägt aber breite Schuppen, der deutliche Ventral-Fortsatz Schuppenhaare.—Eine sonderbare Ausbildung findet man bei *Aegeria* (Aegeriid.) (Fig. 14): Die ventrale Partie der Tegula ist eigenartig verschoben, der Ventralfortsatz nur in Form eines kleinen Höckers ausgeprägt, sein Schuppenhaar-Busch ist kürzer als der dorsale, erreicht anscheinend nicht das Frenulum; starke Haarbüsche an der Wurzel des Vorderrandes des Vorderflügels haben wohl auch hier die vermutete Funktion der Tegula bei der Flügel-Koppelung übernommen.—Bei *Sitotroga* und *Gelechia* (Gelechiid.) wie bei *Mompha* (Momphid.) (Figs. 15–17) sind Ventralfortsatz und sein Schuppenbusch kräftig entwickelt und abgesetzt; der dorsale Fortsatz ist zwar wenig ausgezogen, trägt aber einen langen Busch breiter Schuppen.—Bei den Tortricidae (*Tortrix*, Fig. 18) und *Laspeyresia* (Fig. 19) ist auch der Dorsalfortsatz schon verlängert; sein Schuppenbusch ist im Verhältnis zu ihm kürzer.—Bei *Zeuzera* (Cossid.) (Fig. 20) findet man entsprechend der relativ ursprünglichen Stellung der Familie eine wenig differenzierte Tegula: Dorsal-und Ventralecke sind wenig ausgezogen, die Schuppenbüsche wenig von der Gesamtbeschuppung abgesetzt, nur durch Haarschuppen im Gegensatz zu den sonstigen spatelförmigen Schuppen weicht der Ventralbusch ab. Auch *Zygaena* (Zygaenid.) zeigt keine ausgesprochene Fortsatzbildung, die Tegula ist ziemlich gleichmässig mit Haarschuppen besetzt, die ventral wenig verlängert sind.—Bei *Castnia* (Castniid.) (Fig. 21) sind beide Fortsätze gut abgesetzt, beide mit recht kurzen Büschen sehr breiter Schuppen bekleidet.—Bei *Eurrhypara* (Pyraloid.) (Fig. 22) ist auch der Dorsalfortsatz sehr stark verlängert; beide Fortsätze sind mit langen Haarschuppen besetzt; die breiten Schuppen finden sich nur in der Mitte der Aussenseite des Zentralkörpers. Bei einer anderen Pyraloide, der neotropischen *Casuaria*, kann man, abgesehen von einer starken Absetzung des Ventralfortsatzes, keine auffälligen Besonderheiten finden, obgleich hier das ♂ ein hypertrophisch entwickeltes Frenulum aufweist; die Flügelkoppelung wird bei dieser Gattung durch besondere Einrichtungen an Frenulum und Retinakulum verstärkt, über die Barth (1955) berichtet hat.—Bei den nun folgenden Macrofrenatae sind bei den Familien, denen das Frenulum primär fehlt, die Tegulae unterschiedlich entwickelt. *Endromis* (Endrom.) (Fig. 23) wie auch *Eudia* (Saturn.) haben wenig ausgebildete Fortsätze, die Büsche an ihnen sind kurz und bestehen aus ventral wie auch dorsal wenig abgesetzten Haarschuppen. Dagegen findet man an *Malacosoma* (Lasiocamp.) (Fig. 24) Tegulae mit stark verlängerten, mit langen Haarbüschen versehenen Fortsätzen.—Bei den Familiengruppen mit primär entwickeltem Frenulum ist meist der dorsale Fortsatz stark verlängert, der ventrale gut abgesetzt, aber weniger verlängert, so bei *Mimas* (Sphing.) (Fig. 25), *Cymatophora* (Cymatoph.) und *Boarmia* (Geometr.) (Fig. 26). Bei *Epicopeia* ist beim ♀ der Dorsalfortsatz länger, der ventrale kürzer als beim ♂. *Callidula* (Callidul.) zeigt beide Fortsätze deutlich abgesetzt, beide sind beim ♂ merklich

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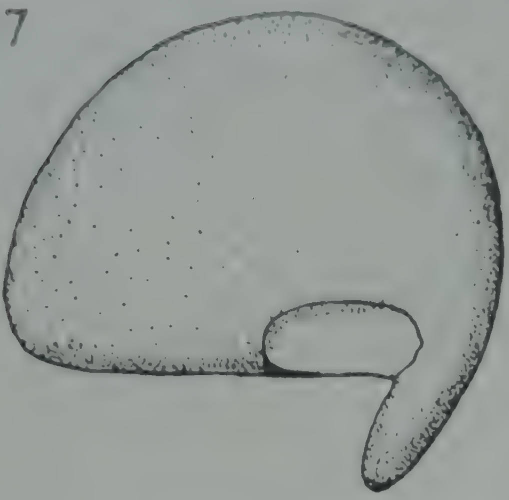
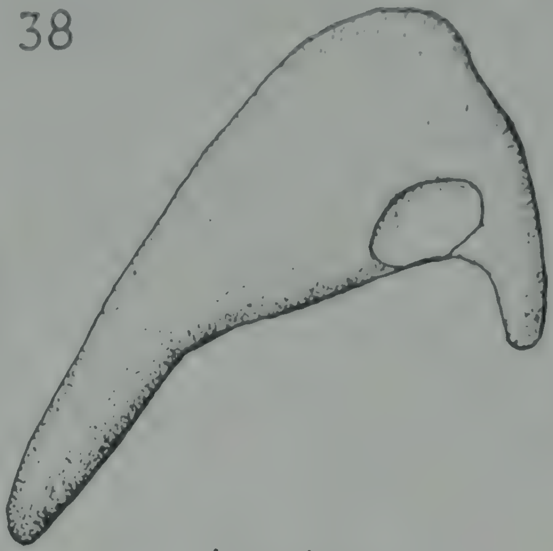
Figs. 25–36. Tegula. 25, *Mimas tiliae* L.; 26, *Boarmia punctinalis* Sc.; 27, *Ratarda tertia* Strd.; 28, *Syntomis phegea* L.; 29, *Lymantria monacha* L.; 30, *Phytometra gamma* L.; 31, *Euschemon rafflesiae* Macl.; 32, *Ochlodes venata* Br. & Gr.; 33, *Iphiclides podalirius* L.; 34, *Parnassius mnemosyne* L.; 35, *Pieris* brassicae L.; 36, *Acraea vesta* F. (Acraeinae).

37



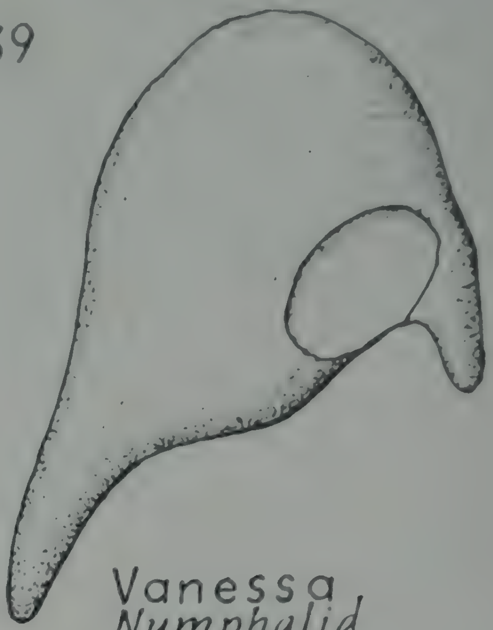
Danaus
Danaid.

38



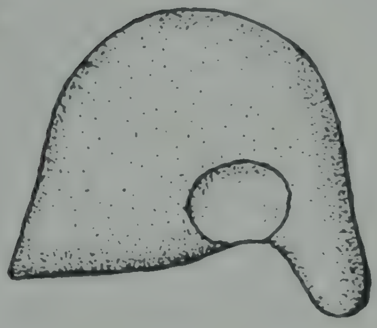
Apatura
Nymphalid.

39



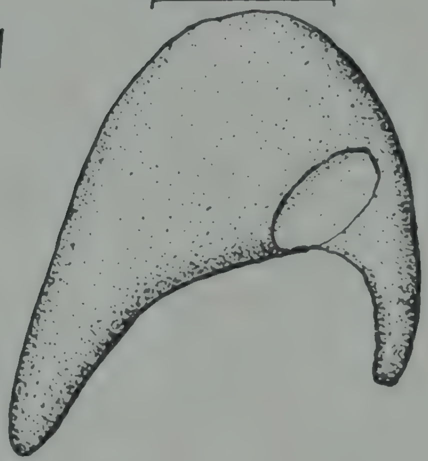
Vanessa
Nymphalid.

40



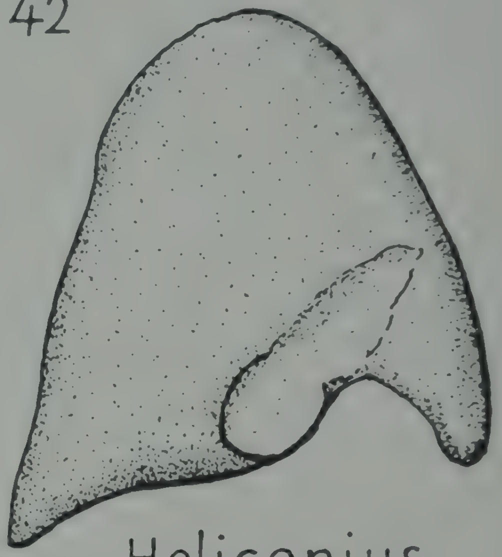
Clossiana
Nymphalid.

41



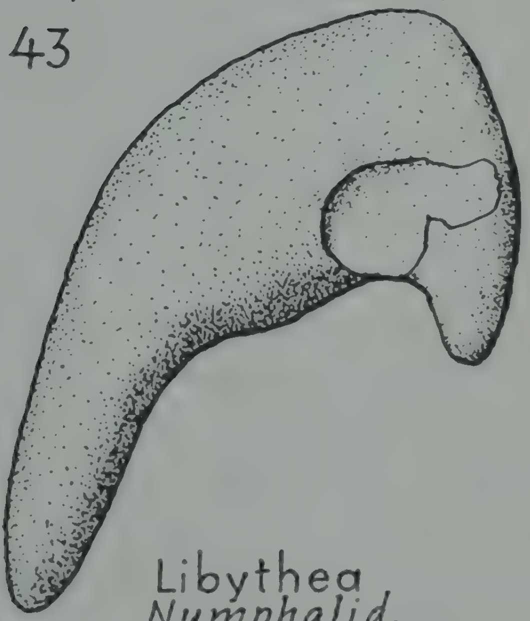
Argynnis
Nymphalid.

42



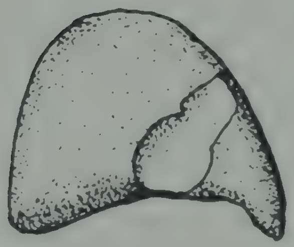
Heliconius
Nymphalid.

43



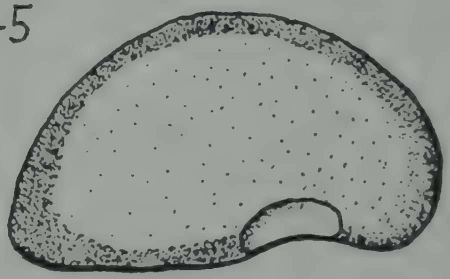
Libythea
Nymphalid.

44



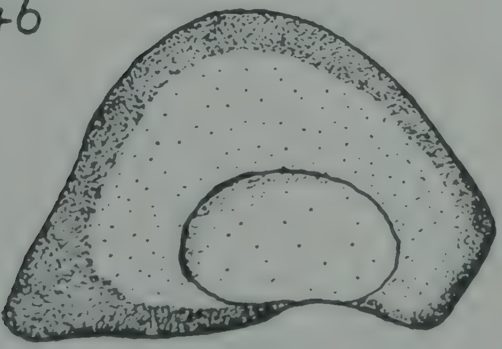
Morpho
Nymphalid.

45



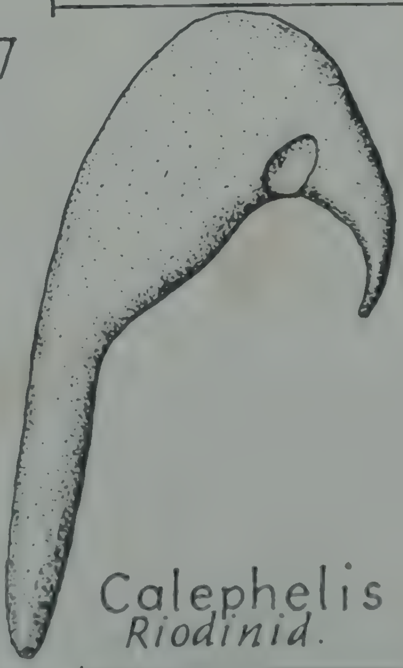
Coenonympha
Nymphalid.

46



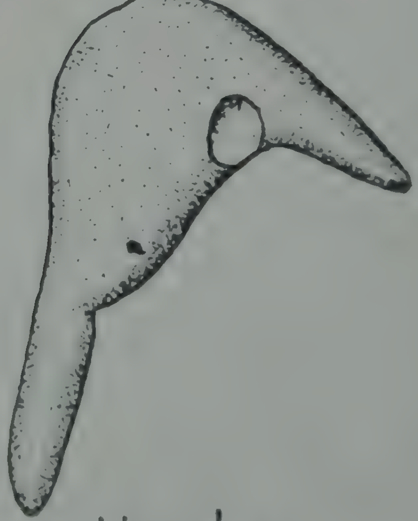
Oeneis
Nymphalid.

47



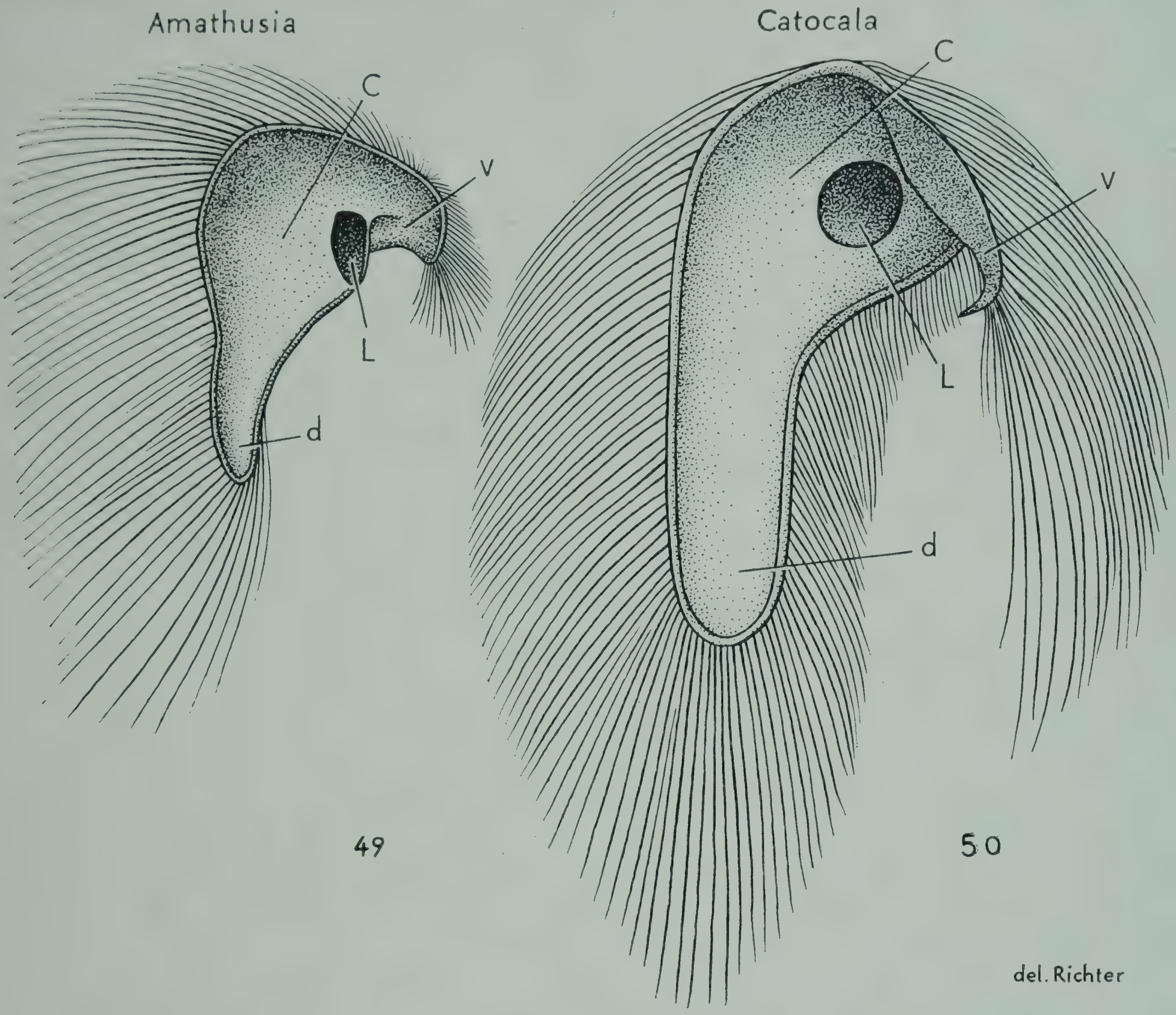
Calephelis
Riodinid.

48



Heodes
Lycaenid.

schlanker als beim ♀ —Ganz abweichend ist die Tegula der auch sonst recht abseits stehenden *Ratarda* (Ratard.) (Fig. 27) gebaut: beide Fortsätze sind kaum angedeutet, die ventrale Ecke ist schwächer sklerotisiert, anscheinend in Rückbildung begriffen. Die Schuppenbüsche sind relativ wenig von der übrigen Behaarung abgesetzt und recht kurz. —In der grossen Familiengruppe der Noctuoidea begegnet man einer ziemlich einheitlichen Ausbildung der Tegula; der Dorsalfortsatz ist meist stark verlängert, der ventrale gut abgesetzt, beide mit langen Haar-oder Schuppenbüschen, so bei *Syntomis* (Syntomid.) (Fig. 28), *Phytometra* (Noct.) (Fig. 30) und *Lymantria* (Lymantr.) (Fig. 29). Bei *Pterothysanus* (Lymantr.) ist der Ventralfortsatz kaum angedeutet, bei *Anthela* (Lymantr.) aber kräftig entwickelt. Bei allen Subfamilien der Noctuidae ist die Tegula ziemlich einheitlich gebaut, der Busch des Ventralfortsatzes wenig kürzer als der stark entwickelte dorsale; auch etwas abseitig stehende Unterfamilien wie die Cocythiinae und Agaristinae zeigen keine Sonderbildungen.—



Figs. 49–50. Tegula. 49, *Amathusia phidippus* L. (Nymphalidae, Amathusiinae); 50, *Catocala elocata* L. (Noctuidae).

Die waagerechte Linie unter jeder Figur entspricht einer Länge von 1 mm, wo nicht 0,1 (mm) beigefügt worden ist; diese Striche bezeichnen die Vergrößerung der dargestellten Organe.

Wie Jordan nachwies, gleicht die Tegula der Hesperiidae in der Lage ihrer Anheftungsstelle der der Heterocera; bei *Euschemon* (Fig. 31), der einzigen Gattung, die beim ♂

← Figs. 37–48. Tegula. 37, *Danaus archippus* F. (Danainae); 38, *Apatura iris* L. (Apaturinae); 39, *Vanessa cardui* L. (Nymphalinae); 40, *Clossiana selene* Schiff. (Nymphalinae); 41, *Argynnis paphia* L. (Nymphalinae); 42, *Heliconius melpomene* L. (Heliconiinae); 43, *Libythea carinenta* Cr. (Libytheinae); 44, *Morpho aega* Hb. (Morphinae); 45, *Coenonympha pamphilus* L. (Satyrinae); 46, *Oeneis jutta* Hb. (Satyrinae); 47, *Calephelis borealis* Gr. & Rb.; 48, *Heodes tityrus* Poda.

ein Frenulum besitzt, liegt diese Stelle aber am Ventralrande wie bei den Rhopalocera. Innerhalb der Familie ist die Ausbildung des Ventralfortsatzes recht verschiedenartig; Bildungen wie bei Fig. 31 findet man auch bei *Pyrrhopyge* und *Aegiale*, Rückbildung des Ventralfortsatzes deutet sich bei *Ochlodes* (Fig. 32) an.

Innerhalb der Rhopalocera kann man eine recht verschiedenartige Gestaltung der Tegula beobachten, sogar innerhalb der Familien. Bei den Papilionidae (*Iphiclides*, Fig. 33) besitzt sie eine Form, die von der der Heterocera wenig abweicht, nur ist die Anheftungsstelle des Ventralfortsatzes weniger sklerotisiert; die Anheftung am Thorax ist solider, die Loslösung von ihm schwieriger durchzuführen, leicht bricht dabei der Ventralfortsatz ab. Bei *Parnassius* (Fig. 34) und *Doritis* ist der Ventralfortsatz sehr breit, mit einer Tendenz zu seinem Einbau in den Zentralkörper. Bei *Baronia* sind Fortsätze kaum angedeutet, parallel der auch sonst recht abseitigen systematischen Stellung der Gattung.—Alle bisher untersuchten Pieridae besitzen einen stark entwickelten Ventralfortsatz. Aber bei *Pieris* (Fig. 35) ist er im Gegensatz zum sonst stark sklerotisierten Zentralkörper ganz weichhäutig geworden und deutet dadurch seine künftige Rückbildung an.—Innerhalb der Nymphalidae findet sich die weitestgehende Vielgestaltigkeit der Tegula. Bei *Libythea* (Fig. 43) ist, abgesehen von der Anheftungsstelle, eine merkliche Aehnlichkeit mit der Tegula der Heterocera deutlich. Auch *Apatura* (Fig. 38) und *Vanessa* (Fig. 39) entfernen sich in der Gestalt wenig von diesem Typus. Bei anderen Unterfamilien sind dagegen die Forsätze stark verkürzt, wenig vom Zentralkörper abgehoben, ausgeprägt namentlich bei *Danaus* (Fig. 37), *Leucothyris*, weniger bei *Tellervo* (Danainae) und besonders bei *Acraea* (Fig. 36) und *Actinote* (Acraeinae). Wie einander nahestehende Genera sich in der Tegula-Form beträchtlich unterscheiden können, zeigen *Clossiana* (Fig. 40) und *Argynnis* (Fig. 41). Die ausgesprochene Verschiedenheit dieses Sklerites bei *Amathusia* (Fig. 49) und *Morpho* (Fig. 44) macht deutlich, wie wenig die Amathusiinae mit den Morphinae zu tun haben. Besonders auffällig ist bei den grossen Flügeln der *Morpho*, dass die Tegulae nur winzige Schüppchen ohne abgesetzte Fortsätze, ohne längere Schuppenbüsche, sind. Bei den Satyrinae *Coenonympha* (Fig. 45) und *Oeneis* (Fig. 46) sind keine abgesetzten Fortsätze mehr vorhanden; bei ihnen ist die ganze Innenseite der Tegula dünnhäutig geworden, abgesehen von einer stärker sklerotisierten Randzone. Dieses Kennzeichen findet man auch bei den Gattungen, die wohl ausgebildete Fortsätze besitzen, wie etwa bei *Pararge*.—Die Riodinidae (*Calephelis*, Fig. 47) und die Lycaenidae (*Heodes*, Fig. 48) zeigen eine relativ ähnliche Tegula, die (abgesehen von einigen mehr isoliert stehenden Genera) durch lange, schlanke Fortsätze ausgezeichnet ist. In dieser geringen Fortsatz-Rückbildung erweisen sich die beiden Familien ebenso wie in der fehlenden Vorderbein-Rückbildung des ♀ ursprünglicher als die meisten Nymphalidae. Indessen wird bei einigen Gruppen der Lycaenidae, die auch sonst als abseits stehend erscheinen (*Pentila*, *Mimacraea*), auch ein Fehlen der Fortsätze beobachtet.

LITERATURVERZEICHNIS

Barth, R. 1955. Männliche Duftorgane brasilianischer Lepidopteren. 6. Mitteilung: Casuaria physyphora (Fld.). *Anais Ac. Brasil Ciénc.* 27: 231–240.

Jordan, K. 1928. On *Eumesia semiargentea* Feld. (1867) with remarks on the nomenclatorial status of artifacts and on the wing-bases and tegulae of Lepidoptera. *Novit. Zool.* 34: 141–146.

von Kéler, St. 1955. Entomologisches Wörterbuch. *Akad.-Verlag Berlin*: 568–569.

Kirby, W., & W. Spence. 1826. An introduction to entomology. Vol. 3, p. 620.

Prochnow, O. 1928. Mechanik des Insektenfluges. *In*: Chr. Schröder, Handbuch der Entomologie, vol. 1, p. 549.

Riley, C. V. 1892. On certain peculiar structures of Lepidoptera. *Proc. ent. Soc. Washington* 2: 305–312.

Snodgrass, R. E. 1909. The thorax of insects and the articulation of the wings. *Proc. U.S. Nat. Mus.* 36: 511–595.

Townsend, C. H. T. 1934. Manual of entomology, vol. 1, p. 182; vol. 2, p. 67, 76, pl. 3, Fig. 9.

Weber, H. 1926. Der Thorax der Hornisse. *Zoolog. Jahrb. Anatomie* 47: 1–99.

Weber, H. 1933. Lehrbuch der Entomologie. p. 146, 181. Jena, G. *Fischer*.

Caterpillars as Botanists

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ABSTRACT

Plant-feeding caterpillars show a great range of food choice, some feeding on almost any green plant, many limiting themselves to a species, a genus, or a group of closely related genera, while a number seem at first merely erratic in their food choices. Those that are somewhat fastidious may give light on plant relationships, and a common choice of food may indicate relationships in the caterpillars. Thus many nymphalids feed on the nettle family, in its broadest sense, suggesting that the plants that many botanists now divide into three or four families are really closely related; also that Libythea, *which some entomologists make a separate family is a true nymphalid, feeding on* Celtis *as it does. Similarly the* Pieris *group agrees with the botanists that the Capparidaceae are close to the Cruciferae, and the argynnines group together the Violaceae and Passifloraceae, with some but not all botanists. But they also, in five separate cases, group the Onagraceae and Vitaceae, which I think no botanists would accept. The association of early papilios* (troilus, *with its primitive feet) with the Magnoliaceae and Lauraceae, and others with the Anonaceae and Aristolochiaceae, suggests that they developed when these were the dominant families of plants, at the beginning of the Cretaceous. But at that time the saturniids were doubtless more advanced, for it is the specialized* Samia *and* Callosamia *that choose these foods. Other cases may be discussed, why groups of pierids have gone over to mistletoes and* Salvadora, *and why in South America the giant swallowtail eats pepper; also anomalous cases that must be due to mere taste, and not true plant relationship, such as the black swallowtail group:* Citrus, *Umbelliferae, Compositae, instead of their ancestral Lauraceae.*

I am not claiming that caterpillars are very good botanists. But they do exercise some choice of food as caterpillars, and in many butterflies and moths the adults also exercise choice in laying their eggs. It is clear that this is based almost entirely on two features, the texture and the flavor (taste and smell-taste) of the tested food. This latter is no doubt the important factor, and while not final, will add a neglected item in the characters by which we classify the plants.

In the present report I shall consider only those caterpillars that feed on the green higher plants, neglecting the scavengers, the feeders on fungi, and the predators, which after all are a small minority of our species. Among these there are three levels of choice: some make little choice, eating anything that is not grossly unsuitable, such as plants with poisons and sticky gums, or ones that feed on a great variety, perhaps only distinguishing between monocots, dicots, and conifers. These are the *Polyphagous* species. The other extreme are those that feed only on a single type of plant, a single genus or even only a few species of a genus; these we call *Monophagous.* And finally are those in between, and they are the ones that interest us today; these are the ones that eat some variety of plants, but yet are selective, some taking a list that may be more or less related, others making a choice that seems arbitrary. These are the *Oligophagous* species. And among these, the ones that make a seemingly illogical choice are the most interesting.

Of course, as I just said, the caterpillars do not choose on the basis of what we should call relationships, but on taste, and their behavior throws light chiefly on some hidden features of chemistry. This choice may be made either by the butterfly when she rasps the leaf surface to test it before laying the egg, or by the caterpillar; but the two tests would tend to have the same answer; for an egg laid on an unsuitable food, or a useful food neglected, would both be needless wastes.

Now for some examples to show how good botanists the caterpillars may be. The cabbage butterflies (Pierini in the restricted sense) practically limit themselves to two families of plants which we agree are closely related, the Cruciferae, chiefly in the temperate zone, replaced by the Capparidaceae in the tropics. And there are several species that will feed on both. Here the caterpillars agree with the botanists. But both our common cabbage butterfly and the related European *Pieris brassicae* may be found on the garden nasturtium, a member of another family, though to us also with a similar taste. We must ask the botanists if Tropaeolum can perhaps be nearer the Cruciferae, but the answer is almost certainly no.

Again we have the milkweed butterflies (Danainae). Here practically all feed on the milkweed family, with a few on the very closely related Apocynaceae. Again the caterpillars and botanists agree, but again there is an exception to be explained, for the two primitive genera whose foods are known eat Ficus instead. We can find other examples where milky-sap plants are treated as a group.

And in contrast, we have a case where the caterpillars are insistent, yet I think no botanists will accept their judgment. In half a dozen cases the Vitaceae (grapes) and Onagraceae *plus* Lythraceae are paired together, by single species or closely related ones. Here are the outstanding examples:

Alypia octomaculata on grape, Japanese Ivy, etc.; *A. langtonii* on willow herb.

Eudryas grata on grape; *E. unio* on swamp loosestrife.

In the sphinxes, several examples; *Pholus* mostly on the grape family, but *P. fasciatus* and *eacus* on Onagraceae (Jussieua).

Amphion nessus, *Deidamia inscriptum* and *Sphecodina abbottii* on grape; the very closely related *Proserpinus* species on fire-weed.

And there are a few more cases a little less strict where grape and Onagraceae are leading members of a somewhat wider choice; thus *Darapsa myron* on grape, *D. versicolor* on several plants including swamp loosestrife, but not grape, so far as I have seen report. The species of Celerio and Pergesa make further similar cases, chiefly in the Old World, but go over also onto the madder family (Rubiaceae), which is another interesting story.

Another diluted case is in the geometers, where *Lygris diversilineata* and *gracilineata* feed on grape, while several members of the immediate group, including the rather closely related *Eustroma nubilata*, are onagraceous feeders.

And finally the curious case of the pyralid, *Desmia maculalis*. It is a well known grape feeder, even perhaps a minor pest; but Cornell has a specimen reared by Miss Murtfeldt from evening primrose.

These last cases lead us over into a group whose choice seems merely erratic, even crazy in cases, for we often cannot see any reason, taxonomic or ecological, for the choices. Some may indicate relationships that the botanists have misunderstood, others may indicate that caterpillar taste is as erratic as ours,—such as the oyster ana the oyster plant, or the two totally different things we call pepper.

In the border zone is the case of the argynnids and heliconids, for here botanists disagree. As a group they feed on the violet and passion-flower families, with several species feeding on both; some botanists put these famillies side by side, others in different natural orders. In this case I suspect the botanists who agree with the caterpillars are right. But when a lot of Acraeinae went over to the Compositae, it was too far.

But there are some more improbable cases. For instance *Papilio thoas* feeds, with a hundred relatives, on the orange family (Rutaceae), but in Guiana I also found it commonly on Piper. This seems an odd choice, since Piper to our taste has none of the orange aroma; but the ecology gives us a hint. Piper is the commonest under-shrub in the forests where the tropical Citrus trees occur, and a caterpillar that dropped to the ground, as they will do, is saved the trouble of a long climb back if he becomes adapted to Piper. This may not be the true reason, but it is the one that struck me on the spot.

In the *machaon* group the changes of food opened large new areas to them; starting with the orange family, which *machaon* itself may still sometimes eat (also *rudkini* in the Southwest), the change to Umbelliferae opened a wide zone of the north, where there are no other Papilios; and the second change (by *oregonia*) to Compositae, opened a great arid area of the northwest. In this case there is the aromatic flavor in common, and the shift is not yet complete; for *rudkini* may be no more than a population of *oregonia*, and I once found *asterias* cheerfully feeding on a Cosmos in our garden.

Papilio turnus has also done something of the sort, and thereby much widened its chance for a meal; for it belongs to the very primitive *troilus* group in caterpillar structure, and instead of being limited to the ancient Magnoliaceae and Lauraceae, has a wide choice of trees and shrubs, a few of them not even aromatic.

There are other cases where an abrupt change of food may be producing the practical isolation needed to change a form into a species, where there is no island or mountain barrier to serve. Thus three Thanaos (Erynnis now by a specially violent shift of names) occupy almost identical areas, also ecologically not too different, for all three choose areas of mixed grass, weeds, undershrubs and some trees. These are *persius* on willow, *lucilius* on columbine, and *baptisiae* on legumes, mostly on Baptisia. The foods are certainly totally unrelated and so far as we can see they are different just to *be* different.

There are other cases. A striking one is *Adita chionanthi*, which feeds on Oleaceae (Chionanthus and ash), and Triosteum in the honeysuckle family. Perhaps we should ask the botanists, but these families seem unrelated, and it may again by a protection from interbreeding to protect two populations on the point of becoming species (the eggs and larvae are already different, though I can see nothing in the adults.)

The caterpillars may also give us light on the history of the order Lepidoptera and its subdivisions.

We know from the record that about the beginning of the Cretaceous time many of our modern families of flowering plants became important, and the older types of plants became extinct with a few exceptions like the gingko. Now considering that foods in the caterpillars tend to be rather specific, we may distinguish three zones of time. Before this period all the common available foods were types now extinct. So any caterpillars feeding on ordinary leafy plants had to become versatile and find something else or starve. No doubt, then, the monophagous types and the fussy ones generally became extinct, and of these early types only the polyphagous could change their food and survive. Second, those dominant at the very beginning of this period found just a few of the modern dominant families already there, and would be very likely to adapt to such families as the Magnoliaceae, Lauraceae, and Anonaceae. It would seem that the Aristolochiaceae were also there, probably already becoming adapted to less truly forest areas. There were of course a few more families that survive from this period, but they would have been scarce either then or now. The conifers are a separate problem I may later have time to consider, but it would seem that they and the lower plants had little to offer the caterpillars. They may perhaps have been reduced to a very low level by the arid Triassic period. In any case almost everything that feeds on them is very modern in type and relations, often mere odd species of more normal genera, like *Sphinx pinastri* and many geometers on conifers, or the four or five Papaipemas on ferns.

Finally groups that got their real development later would have the wider list of Cretaceous to modern families to choose from.

So we should expect ancient types to be general feeders, intermediate ones to be monophagous or oligophagous on a very few families, modern ones to show here and there earlier food-habits showing through the more recent erratic shifts. And this is what we find.

The best example is Papilio, with its relatives. Here there are three main groups of species, which we all accept (due to Rothschild and Jordan originally). The most ancient members of one (which still live in a shelter and have prolegs with a ring of hooks) feed on Magnoliaceae (*palamedes*) and Lauraceae (*troilus*). A few Old World members of the series also have Lauraceous foods. The second group, with many outlying small genera, feed on the Aristolochiaceae, and the third on Lauraceae and Anonaceae. The list says, as plainly as such things can, that Papilio was established and already divided in three sections, before the big radiation of flowering plants in the Cretaceous. After this there are the usual food radiations and one of them must have been early, for the great majority of the first group now eat the orange family all over the world, from New York to the Argentine, and from California to New Caledonia and Fiji.

Part of the later adventures can be explained; the *machaon* group as already mentioned; one kite (*podalirius*) went from Anonaceae to Rosaceae, and so has entered Europe; another in South America has gone to Vitex (Verbenaceae). One "Aristolochia" Papilio has survived in Madagascar, now eating Combretum, but none have survived the loss of their host family in Africa. Parnassius has entered the Alpine zone by changing to Sedum. Such changes as these make the caterpillars good ecologists but hardly plant taxonomists.

To go back a step, we come to the skippers. And just as we should we find much more versatile feeding, with little choice of families; only a preference for monocots or dicots. So the Pamphiline skippers and their close relative Megathymus, also the Australian

Trapezitinae, feed only on monocots and so do all the known Castniidae, though they range over many families, from grasses to orchids. But the other subfamilies of skippers and the Cossidae choose the dicots in the same unpatterned way. Below this we cannot go, for there are no feeders on green plants on the main line of descent till we reach the bottom. The Micropterygidae feed on liverworts, and probably have done so since the Permian Age.

Turning to the more recent families, we find in both the Pieridae and Nymphalidae ancient associations of major groups with single families (or related pairs) of plants. Take the Pieridae; here members of both subfamilies feed on legumes, and this may or may not be significant, for that is a dominant family that could be chosen twice a little later. But the strikingly different Dismorphiinae of the two hemispheres must have been separated for a very long time, and both eat legumes. The cabbage butterflies, which we have discussed, make a second major group, and the orange tips, which belong with them, are in structure the most primitive Pierinae, rather than the legume feeders. Then there is a third group (mostly tropical) that have curiously taken to the mistletoes. This is nearer to the cabbage butterflies than to the legume group, in fact the white species used to be put in Pieris.

Three large groups, each of many genera, and each evidently monophagous for a very long time, clearly indicate an old family, but one not older than the Cretaceous. (I wish we knew more about Baronia).

The Nymphalidae are an equally striking case. Here two foods are evidently very ancient, older than some of the subfamily separations; for the vanessids, our Apaturini, libytheas and various further mostly tropical groups choose the Urticaceae, while the argynnids, with their related Heliconiinae and old-world Acraeinae, take the violets and passion flowers. And the urticaceous food must be very ancient, for some would even make a separate family of Libythea. We have one dating point, for a Miocene fossil (Prodryas) is a good enough Hypanartia, and must have fed on something like Cecropia, mulberry, or bread-fruit.

For the larger subdivision of the family, foods are again significant. The danaids feed on milky-sap and poison plants (which go together in many other cases); the ithomiids on Solanaceae, satyrs with Brassolinae and Amathusiinae on monocots,—grasses in the temperate zone, often palms in the tropics. And this is about all the caterpillar foods tell us here; that the Nymphalinae split down the middle very early, the Danainae and Ithomiinae are good subfamilies, and that the giant Brassolinae and Amathusiinae have some connection with the satyrs, as we judge also from structures and patterns.

In these two groups again we find the odd types that have gone off to an unrelated food, and in some cases have opened a new field thereby. Thus the California pine-feeding *Neophasia menapia* has a tremendous advantage over *N. terlootii* which is said to eat mistletoe as it should. One genus of the cabbage group in the old world (Teracolus, now called Colotis) has gone over to the wide-spread shrub Salvadora, and now is dominant both in tropical Asia and Africa. The botanists put Salvadora nowhere near the Capparidaceae; can they be persuaded to look again?

The Sphingidae again show the presence of food types established long before the separation of present genera, or even perhaps subfamilies, but the matter is even more complex. At most we can say at the moment that the food groupings in the Semanophorae run right across the group lines as Rothschild and Jordan laid them down. The same is true of the caterpillar forms and patterns, and I think that end of the family will have to be totally rearranged.

In the Sphinginae (Acherontiinae of R. and J.) of the Asemanophorae there is obviously a single basic food, the Oleaceae, shared by at least eight genera, and the chief switch (to the Solanaceae) makes no sense botanically, ecologically, nor yet in flavor to our taste. But members of four separate genera (Acherontia, Coelonia, Phlegethontius and Amphimoea) have made the switch, though members of at least three still use the Oleaceae also. The families are not too far apart in traditional botany (Engler, etc.) but families which this series of sphinxes never eat lie between. The Bignoniaceae, which several types do eat, also lie in between (*Atreides plebeius*, *Ceratomia catalpae*, *Euryglottis* and an odd *Phlegethontius*). Brahmaea, which Jordan considers ancestral to the Sphingidae, also feeds on Oleaceae.

The Smerinthinae, which we consider a branch of the same main line, have evidently gone adventurous, eating almost any trees and shrubs of the dicots; but three primitive genera (Compsogene, Protambulyx, and Oxyambulyx) agree on the Anacardiaceae (cashew), and so fit better in their preferences with the Semanophorae.

The Semanophorae again have a group of much preferred families, which would seem unrelated. First of all come the Rubiaceae, preferred by some 20 genera, all up and down the series (except for the Erynnyis group—the Sesiicae,—which also have distinctive caterpillars). As these three genera are primitive in preserving distinct primary setae, we cannot be sure that the Rubiaceae were really the original food of the series; these three agree on the Apocynaceae instead, along with some of the more advanced Semanophorae. Next come the pair already discussed, Vitaceae and Onagraceae. This choice is less widespread than that of the Rubiaceae, but is widespread in the first two of R. and J.'s subfamilies, and are an important second choice in the third (Choerocampinae), at least its old-world members. Evidently either the grapes and willow herb have more in common with the Rubiaceae than the botanists accept, or else our subdivision needs recasting. I believe that the answer is "both". The three families lie on pages 129, 168 and 210 of the botany at my elbow (Gunderson's "Families of Dicotyledons", which follows the Engler system). The other distinctive family of dicots is the Euphorbiaceae, preferred by *Erynnyis ello* and accepted by a few others. But the most surprising is that only in the old world a whole group of genera, mostly grouped about Theretra, have gone clear over to the monocots, and feed on the aroids (elephant ear and others). Here all we can see is that they are immune to some powerful poisons,—a curious link between them and the poisonous but often edible euphorbs. In sum the Semanophorae in an interlocking pattern choose the Apocynaceae (with asclepiads in a smaller way), Rubiaceae (with a few on the related honeysuckles), Vitaceae, Onagraceae, Euphorbiaceae and arums. What on earth do these families have in common?

We have rather passed over the conifers. Geologically these are a little older than the flowering plants, and should locate a time-point on our genealogy as the Magnoliaceae and their group do, but a little older. In fact we find no such link. Most conifer feeders are clearly close relatives of feeders on dicots, usually polyphagous ones, so we must decide that their choice of the pines is secondary. The only link that one can suspect is more significant, is a weak one in the saturnioids. Here the conifer food is dominant in no group, but scattered through the family and may just possibly have lasted since before the higher plants arose, for some of these pine feeders are primitive and aberrant forms. The list is chiefly: Eacles (sometimes, but with a special method of feeding), *Citheronia sepulcralis*, Coloradia, a single Dirphia from Haiti, Graellsia. But there is in all the Lepidoptera no conifer feeder that is even *probably* one from the beginning, no cycad feeder, and no gingko feeder at all. As to the scattered families, of a genus or two each, that botanists place below the Magnoliaceae, I have no information that they are the hosts of anything. Some one ought to make a study of Illicium from our south and Degeneria from the Fiji Islands.

There is a final point which the caterpillars may be able to answer, but we do not have enough data. That is whether the monocots are a single series or have arisen separately from two or more points in the dicot series. What little we see suggests that they are homogeneous, notably the Castniidae, which eat anything from grass to orchids. But there is one suggestive point. The pickerel weeds have been suggested as perhaps nearest to the dicots; and we have the case of Arzama, Bellura and Sphida, probably a single genus and certainly very close relatives. Their foods are cattail, water lily, and pickerel weed. Meropleon, a little more distinct, feeds on the coarser grasses, including sugar cane. But the somewhat more distinct relatives are so varied that more likely the grouping is meaningless.

Color Pattern in the Lepidoptera

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ABSTRACT[1]

Studies of color patterns of Lepidoptera, mainly those carried on in the USSR, are reviewed, and some remarks on color patterns in the Vertebrata are appended.

A principal method of studying wing-pattern is that of building up series of individual pattern components. To find the direction of the evolution of a given component, a comparison of several series of it is necessary; no single series may reveal the evolutionary direction.

Three broad, transverse stripes or systems of symmetrical structure, enterna, media, *and* basalis, *are the main components of the prototype valid for the primitive Lepidoptera. In the medio-discal prototype of the Heterocera, the medial system becomes dominant, the external system loses its symmetrical structure, and a system of three discal spots is added. The general rhopalocerous prototype, as compared to the preceding, shows three peripheral stripes instead of two and shows the extramedial position of one of the discal spots instead of the intramedial position. The nymphaloid prototype differs from the preceding in having a series of eye-spots. Two more prototypes of secondary importance are added to the mediodiscal one.*

Some 28 wing-patterns of the Heterocera and Rhopalocera, chosen from a much greater number, are reduced to the prototypes described above.

The biological importance of cryptic patterns has been shown by a number of authors. The maximum resemblance to models and the maximum modifications of patterns are often concomitant. Stereomorphism, i.e., the presence on the wing of two dimensional images of three dimensional models, relieves the flat wing surface and enhances the cryptic effect. Stereomorphic color patterns are not restricted to the Lepidoptera but occur in other animals including Vertebrata. Cryptic effect may be heightened by the green reflection principle; some surfaces of the body, especially shining surfaces, may reflect the green of vegetation and thus become visually as green as the latter.

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The Systematic Position of the Family Thaumastocoridae (Hemiptera: Heteroptera)

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ABSTRACT

The phylogenetic position of the family is reviewed and the conclusion is reached that these insects are cimicoid Hemiptera related to the family Anthocoridae. Instead of possessing very primitive features as has been previously believed, the Thaumastocoridae are in most respects highly specialized.

The hemipterous family Thaumastocoridae is composed of a small number of very rare insects whose relationships within the suborder have been poorly understood in the past. We have recently been engaged in a revisional study of the family[1] and during the course of the work have attempted to better understand the phylogenetic relationships of the family.

The first thaumastocorid was described by Kirkaldy (1908) as a subfamily of Lygaeidae based upon a single specimen (*Thaumastocoris australicus*) collected in Queensland, Australia. The following year Bergroth described a second species in a new genus (*Baclozygum depressum*) from Hobart, Tasmania. Bergroth accepted Kirkaldy's placement of the taxon within the Lygaeidae, noted the highly asymmetrical male genitalia, and interestingly considered the group to be of very ancient lineage. Reuter (1912) raised the thaumastocorids to family rank, giving them Phalanx status in his *schema*, but retaining the family in the series Onychiophora to which the Lygaeidae belonged. Reuter considered the insects primitive but did point out several apparently specialized features.

In 1920 Mr. H. G. Barber of the United States National Museum received a series of very peculiar insects that had been damaging the terminal shoots of the royal palm in Cuba. Barber described these as a new genus and species of thaumastocorid (*Xylastodoris luteolus*), but, as they differed in some important features from the Australian species, he erected a new subfamily to receive the Cuban species. Kormilev (1955) described a fourth genus and species from Argentina (*Discocoris vianai*), also taken on palms, for which he erected a third subfamily. Kormilev also discussed the systematic relationships of the family, pointing out that they were cimicomorphs and thus anticipating several of the conclusions that we have arrived at independently.

It early became apparent to us that, despite previous statements to the contrary, the Thaumastocoridae are not at all related to the Lygaeidae, but rather that, following the classification of Leston, Pendergrast & Southwood (1955), they belong to the Cimicomorpha section of the terrestrial Heteroptera. The evidence for this placement is as follows:

Male Genitalia: Singh-Pruthi (1925) indicates that two basic types of male phallic structure are present in the terrestrial Heteroptera. The first known as the pentatomorph type has the terminal portion of the phallus (endosoma) subdivided into two regions, the conjunctive and the vesica. The second type, that of the Cimicomorpha, has the endosoma undifferentiated into conjunctiva and vesica. Furthermore, in the Cimicomorpha the genital capsule and the parameres are frequently highly asymmetrical, whereas such a condition is very rare in the Pentatomorpha. In the Thaumastocoridae the male genitalia are very asymmetrical. The capsule itself is highly so, often with a flange-like projection near the aperture. In Australian species a single paramere is present; in new world species both parameres are absent. In Australian species the capsule opens either to the right or left side, but in the series studied the direction of opening appears to be constant for a given species. In *Xylastodoris luteolus* both left opening and right opening individuals are present, so that the condition in different specimens appears as a complete mirror image of one another. Kormilev also notes this reversal (which he calls a mutation) in *Discocoris vianai*.

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[1] Drake, C. J., and J. A. Slater. 1957. The phylogeny and systematics of the family Thaumastocoridae (Hemiptera: Heteroptera). *Ann. Ent. Soc. Amer.* 50: 353–370.

Trichobothria: These abdominal sensory structures are generally present in Pentatomorpha, absent in Cimicomorpha. These are absent in all Thaumastocoridae.

Wings: In Pentatomorpha radius and media are separate beyond the basal cell; in Cimicomorpha they are fused. The Thaumastocoridae have the typical cimicomorph fused condition. The venation in general is very much reduced with the hamus, intervannals, and one vannal absent.

Spermatheca: This structure is ectodermal and median in the Pentatomorpha. In the Cimicomorpha it is variously modified, often paired or of mesodermal origin. In the preserved specimens available to us we have not been able to find any evidence of a spermatheca. It is probable that it thus is of mesodermal origin although conceivably absent.

Eggs: In the Pentatomorpha the egg generally possesses micropylar processes and lacks a well developed operculum. In the Cimicomorpha the reverse condition is present. The Thaumastocoridae have no micropylar processes and do have a well developed operculum.

Arolia: Reuter considered these structures to be of great value. They are generally present in the Pentatomorpha and less common in the Cimicomorpha. The Thaumastocoridae have arolia well developed in the Western Hemisphere species but lacking in the Australian forms so that the structure is of no value in evaluating the position of this family.

It seems evident then that the Thaumastocoridae agree in all important respects with the Cimicomorpha and must belong to this group. The question then is, where within this large and heterogeneous group they belong. Reuter (1910) recognized two main subdivisions in his series Anonychia (much like the present day Cimicomorpha), the Cimicoideae and the Reduvioidea. The Thaumastocoridae agree with the former and differ from the Reduvioidea in the following respects:

a. Asymmetrical male genitalia.

b. No abdominal connexivum and attendant connexival sutures.

c. Apparently mesodermal sperm storage organ.

The mesosternum and metasternum apparently are not completely fused, and the coxae are trochalopodous. However, these features have proven to be somewhat variable and do not appear to be of fundamental significance. A more serious question is presented by the presence of a prosternal stridulatory groove in at least some of the Australian species. Usinger (1942) considers this to be a very important character in differentiating the Reduviidae and Phymatidae from the more primitive Nabidae, where the stridulatory groove is absent. Furthermore, there is a most peculiar sensory pad present on the apex of the tibia of Australian thaumastocorids that is also found in the nabid genus *Carthasis*. In view of the general feeling that the Nabidae represent rather primitive cimicomorphs, it is entirely conceivable that the Thaumastocoridae broke off from a nabid stem at an early period and have developed independent genital asymmetry in somewhat the same way the Joppeicidae have developed along a line of genital symmetry. If, however, we follow more conventional procedure and consider the Thaumastocoridae as Cimicoideae, it is necessary to determine whether they are related to the Miriformes as represented by the Miridae and Isometopidae or to the Cimiciformes, comprising the families Cimicidae, Anthocoridae, Microphysidae, etc. Of these families the Microphysidae have symmetrical male genitalia; the Cimicidae are highly specialized parasitic forms, predominantly anthocorid in affinities; and the Isometopidae are very close to the Miridae in nearly all important aspects. Thus the problem is whether the relationship is predominantly anthocorid or mirid. We believe that the Thaumastocoridae are Cimiciformes rather closely related to the Anthocoridae for the following reasons:

a. Ocelli present. b. Porrect head with long gula. c. Lack of veins and cells in the hemelytron. d. Lack of arolia. e. Reduction in number of the parameres. f. Absence of ovipositor. g. Very short basal tarsal segment. h. Obsolete metathoracic scent gland openings. All of the above criteria agree at least in part with the Anthccoridae and differ from the general condition found in Miridae.

In regard to the presumed primitive nature of the family by several authors, it appears to us that like most families of Heteroptera they may be very old, but they certainly are not primitive. The highly specialized rostrum and bucculae, reduction of tarsal segments from three to two, lack of arolia in some forms, marked reduction of the venation of the hind wing and complete lack of venation in the membrane of the front wing, loss of ovipositor, loss of ectodermal spermatheca, asymmetry of the male genital capsule and loss of one or both of the parameres, two instead of three nymphal scent gland openings and reduction of the metathoracic scent gland orifices, all seem to us to indicate that the family Thaumastocoridae is a very highly specialized taxon within the suborder.

REFERENCES

Barber, H. G. 1920. A new member of the family Thaumastocoridae. *Bull. Brook. Ent. Soc.* 15: 98–105.

Bergroth, E. 1909. Vier neue australische Hemipteren-Gattungen. *Deut. Ent. Zeit.* 1909: 328–335.

Kirkaldy, G. W. 1908. Memoir on a few heteropterous Hemiptera from eastern Australia. *Proc. Linn. Soc. N. South Wales* 32: 768–788.

Kormilev, N. A. 1955. Una curiosa familia de Hemipteros nueva para la fauna Argentina. *Revista Soc. Ent. Argent.* 18: 5–10.

Leston, D., J. G. Pendergrast, & T. R. E. Southwood. 1954. Classification of the terrestrial Heteroptera. (Geocorisae). *Nature* 174: 91–94.

Reuter, O. M. 1910. Neue Beitrage zur Phylogenie und Systematik der Miriden nebst einleitenden Bemerkungen uber die Phylogenie der Heteropteren-familien. *Acta Soc. Sci. Fenn.* 37: 1–171.

Reuter, O. M. 1912. Bemerkungen uber mein neues Heteropteren-system. *Ofv. Finsk. Vet.-Soc. Forh.* 54: 1–62.

Singh-Pruthi, H. 1925. The morphology of the male genitalia in Rhynchota. *Trans. Ent. Soc. Lond.* 1925: 127–256.

Usinger, R. L. 1942. A revised classification of the Reduvioidea with a new subfamily from South America. (Hemiptera). *Ann. Ent. Soc. Amer.* 36: 602–618.

Higher Systematics of Shieldbugs (Hemiptera: Pentatomidae)

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ABSTRACT

There is agreement amongst specialists that shieldbugs warrant superfamily status as Pentatomoidea. At family level no two authors agree. The writer is revising the whole complex and as a preliminary defines Pentatomidae. This, with Dinidoridae and Eumenotidae, comprises the higher Pentatomoidea; the three families together are characterised by a diploid number 14, R+M and Cu of hindwings parallel at the basal third, eggs with a pseudoperculum, aedeagus reduced and three pairs of conjunctival appendages lost. Pentatomidae have the pseudoperculum at the top of the egg, a spermatheca with a long narrow and sclerotised duct invaginated within an elongate sac, male 8th segment without recognizable tergum. Included within Pentatomidae are the primitive Diemeniinae (Diemeniini+Mecideini), Cyrtocorinae, Halyinae, Discocephalini, Amyoteinae, Strachiinae and Pentatominae. Groups sometimes included within Pentatomidae but now excluded are: Phloeidae, Canopidae, Aphylidae, Tessaratomidae, Serbaninae, Scutellerinae, Eurygastrinae, Pachycorinae, Acanthosomidae, Urostylidae — some of these groups require increased or diminished status.

The Spotted Alfalfa Aphid and Related Species

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ABSTRACT

The spotted alfalfa aphid, discovered in the United States early in 1954, is a severe pest in many alfalfa-growing areas west of the Mississippi River. Two species closely related to the spotted alfalfa aphid are of relatively little economic importance, though they have been in America much longer. The yellow clover aphid, whose principal host is red clover, has been known here for 75 years and is generally distributed east of, and in a few states west of, the Mississippi River. The sweetclover aphid has been present in some states at least since 1948 and has spread from coast to coast on sweetclover.

These species are widely distributed in other countries, but the spotted alfalfa aphid is more widespread than the other two or than any other closely related species. In its range of distribution it also shows greater variation in diagnostic characters than the other species. Specimens from North America show little variation and appear identical with specimens from Cyprus, Israel, and Morocco.

These aphids are therioaphidine species and are characterized by greatly enlarged fore coxae and the ability to jump. They are of Old World origin, apparently are restricted in feeding to clovers and related Leguminosae, and are selective in their hosts.

Sur la Découverte de l'Hôte Primaire d'un Aphidoidea (Fordinae) du Genre *Rectinasus* et des Générations inféodées à cet Hôte

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RÉSUMÉ[1]

Rectinasus buxtoni *Theob., décrit depuis une quarantaine d'années, était connu seulement par ses générations exilées sur des plantes appartenant, la plupart, à la famille des Composées.*

Mordvilko (1936) pensait que Rectinasus *s'apparentait aux* Forda, *auteurs de galles latérales sur les feuilles des* Pistacia.

Nous avons trouvé sur Pistacia khinjuk *Stocks, dans le sud de l'Iran, une espèce de Fordinae gallicole dont les ailés émigrants renferment des embryons morphologiquement identiques à ceux de* Rectinasus buxtoni *Theob. Les galles causées par cet aphide ont la forme d'un sac allongé, inséré près de la base d'une foliole, au voisinage de la nervure médiane; ce sac est rétréci en pointe à l'apex et il pend à la face inférieure de la foliole. Par sa structure, la galle de* Rectinasus *rappelle beaucoup plus celle des* Geoica *ou de* Slavum lentiscoides *Mordv. que celle des* Forda *que nous connaissons; la fondatrice et l'exuvie de sa larve néonate sont emprisonnées dans la galle (comme cela se produit chez* Geoica; *chez les* Forda, *au contraire, les fondatrices évoluent dans une galle temporaire).*

La première génération à laquelle la fondatrice donne naissance comporte 4 à 10 individus aptères. Ces fundatrigeniae donnent alors naissance à de nombreuses larves qui évoluent vers le stade ailé; en septembre, la galle s'ouvre par une fente longitudinale dont les lèvres s'écartent; les ailés émigrent tandis que les fundatrigeniae encore vivants à cette époque, errent sur la galle pendant quelques jours.

La présente communication apporte la description de la larve néonate de la fondatrice, de la fondatrice adulte, des fundatrigeniae, des ailés émigrants et des larves néonates issues de ces émigrants.

Les formes sexupares et sexuées n'ont pas encore été découvertes.

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[1] Le texte complet a été publié dans *Revue de pathologie végétale et d'entomologie agricole de France* 35(4): 215-231, 25 fig. 1 pl. phot. 1956.

Notes on Indian Aleurodidae (Whiteflies), with Special Reference to Hyderabad

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ABSTRACT

Most of the work done on Indian Aleurodidae deals with collections made in the northern region of the country. In this paper a beginning has been made to study the South Indian forms of this family. Most of the material dealt with here has been collected in Hyderabad, a state situated in the centre of the Southern Peninsula. In all, 22 species are listed in 14 genera. Aleurodes cotesii (*Maskell*) *is redescribed and placed under* Trialeurodes, *due to the presence of submarginal papillae and row of pores. Wherever necessary, existing descriptions are supplemented so as to indicate range in variation of the species. The known distribution and host plants are stated.*

Aleuromarginatus tephrosiae *Corbett on* Tephrosia purpurea *and* Bemisia tabaci (*Genn*) *on* Achyranthes aspera *cause leaf-galls. In the former, the puparia are found in pustuloid "buetelgalls", while* Bemisia *puparia are lodged in conspicuous, round, pinkish outgrowths on the underside of leaves.*

Most of the northern species are found in the southern part of the country as well. Quite a few have a wide range of host-plants. Trialeurodes rara *Singh, originally described from a few specimens on* Breynia *sp., is noted to infest castor* (Ricinus communis) *in Hyderabad on a scale equal to* T. ricini (*Misra*), *a known pest of castor.*

INTRODUCTION

Maskell (1895) described the first five specimens of Indian Aleurodidae from material forwarded by the Indian Museum. In 1903, Peal monographed the oriental species, listing 16 from India. The first comprehensive study of the family was done by Quaintance and Baker (1913–14). Karam Singh (1931) revised the earlier work on known Indian species and described many new ones. Since then this author has been dealing with the bulk of Indian material (1938, 1940, 1945) and with some from Burma (1932, 1933). Except for a few species, the above studies exclusively deal with material collected in the northern part of the country.

In this paper an attempt has been made to study the south Indian forms, especially from Hyderabad State. Twenty two species have been listed in 14 genera. *Aleurodes cotesii*, originally described by Maskell, has been redescribed and placed under *Trialeurodes*. Existing descriptions of some others have been supplemented to indicate the range of variation in the species. The study has confirmed the earlier observation of Karam Singh (1931) that many species are widely distributed in the country, though on a different range of host plants. *Trialeurodes rara* Singh, originally described from a few specimens on *Breynia* sp., has been found to be infesting castor bean on a scale equal to *Trialeurodes ricini* (Misra), a known pest of castor bean.

Genus *Aleurotuberculatus* Takahashi

Aleurotuberculatus psidii (Singh)

This species, placed provisionally under *Aleurotrachelus* (Karam Singh, 1931), was transferred to *Aleurotuberculatus* (Takahashi, 1932), due to the presence of tubercles on the cephalothorax.

Puparia small, tapering in shape, devoid of secretion and occurring singly on lower sides, 4–5 per leaf during January. Widest at junction of thorax and abdomen. Margin reflexed and visible intad of the arched line on subdorsum. Granulations on dorsum crescent and arrow-head shaped. Abdominal ridge constituted of 8–9 smoky tubercles with suture-like markings. Similar tubercles on cephalothorax forming an anchor-shaped figure. In addition 5 pairs of colorless tubercles disposed 2, 1 and 2 each on 1st, 2nd and 3rd pair of legs respectively. Vasiform orifice with rim chitinised and a peg-like spine at caudal end.

Host: *Psidium gauyava.*

Locality: Himayetsagar, Begumpet.

Genus *Dialeurodes* Cockerell

Dialeurodes elongata Dozier

Described from specimens sent from India, this species forms the type for subgenus *Dialurolonga* under *Dialeurodes*. Singh (1931) opines that it bears a distinct affinity to *Aleuroparadoxus* in view of the papillae on the sub-margin and appears to be a connecting link between the two genera.

Host: *Citrus* sp.

Locality: Hyderabad.

Dialeurodes euginae (Maskell)

Collected on *Eugenia jambolana* from Poona, this species was one among the first lot of Indian Aleurodidae to be described (Maskell, 1895). It was redescribed by Quaintance and Baker, 1913–14, who assigned it to *Dialeurodes*. Karam Singh (1931) described the egg and earlier instars.

At Himayetsagar, eggs and immature stages are common on tender leaves during early February. The attacked leaves show pit galls, with a nymph in each depression, attended by ants. *Chilomenes sexmaculata*, *Scymnus* sp. and *Coccinella* sp., present in numbers, act as effective checks. Spiders were also found to be predating after stitching up infested leaves.

The minute clear dots referred to by Karam Singh appear as round papillae and are fairly prominent. The egg chorion is not pentagonally sculptured.

Host: *Eugenia jambolana.*

Locality: Himayetsagar.

Dialeurodes trilobitoides Q. and B.

Taken on *Harpullia* and *Eugenia operculata* from Ceylon, this species was made the type of the subgenus *Rachispora* under *Dialeurodes* by the original authors (1913). Karam Singh (1931) recorded it for the first time from India, while it is known to occur commonly in Ceylon (Corbett, 1926).

Present year-round, especially from September onwards on *Mimusops hexandra*, its favourite host here. Eggs distinctively sculptured with globose protruberances and in clusters on underside of leaf. Nymphs and puparia attached 40–50 per leaf, in rows either side of main veins on dorsal side and attended by ants, severe infestation resulting in yellowing of leaves. The underside of leaves with *trilobitoides* are invariably infested with *Dialeurodes ixorae* Singh.

The margin of some cases is broadly toothed, while the submargin has, in places, two rows of paired pores. The vasiform orifice has no hairs intad.

Hosts: *Mimusops hexandra*, *Achras sapota.*

Localities: Himayetsagar, Begumpet.

Dialeurodes spina Singh

Originally described from few specimens obtained on *Ficus religiosa*, it is abundant on the same host in many parts of Hyderabad from September to February. Puparia brown, convex, oval; found on both sides of leaf; without any secretion and easily dislodged. Infested leaves show yellow patches at site of feeding. Foliage of heavily infested trees shows extensive yellow speckling. The puparia are parasitised.

The thoracic and caudal tracheal folds end in combs and not in pores. The latter were seen clearly only a few specimens (Karam Singh, 1931).

Host: *Ficus religiosa.*

Locality: Bhongir, Begumpet, Secunderabad, Himayetsagar.

Genus *Dialeuropora* Q. and B.

Dialeuropora decempunctata Q. and B.

The authors (1917) described this species from material collected on cinnamon from Ceylon and from mulberry at Lahore, using it as type for the subgenus *Dialeuropora* under *Dialeurodes.* Takahashi (1934), on the ground that the members of the subgenus possessed eminent dorsal pores without evident tracheal breathing folds as in other *Dialeurodes*, raised it to the rank of a genus.

Specimens collected here correspond more to the description of Karam Singh (1931), except for the tracheal folds being fairly distinct and with the lingula visible and excluded. The iridescent bluish secretion makes them easily recognisable. Puparia occur mostly on underside.

Hosts: *Ficus religiosa*, *Euphorbia pilulifera*, *Anona squamosa*, *Anona cherimoya*, Avacado pear, *Cordya myxa*, *Rosa* sp.

Locality: Himayetsagar.

Genus *Aleurotrachelus* Q. and B.

Aleurotrachelus rachispora Singh

Puparia occur singly, at the most 2–3 per leaf on the underside and are dark with white marginal secretion as loose-set white filaments. The minute spines referred to by Karam Singh (1931) are found in a submarginal row and are also distributed on the cephalothorax. Margin reflexed. In specimens obtained from *Tamarindus indicus*, the lingula is similarly shaped as the vasiform orifice, which is sub-elliptic, while in those from *Euphorbia* the lingula corresponds to Singh's description.

Hosts: *Cassia auriculata* (July); *Eurphorbia pilulifera* (Dec.); *Tamarindus indicus* (Feb., July).

Locality: Himayetsagar.

Aleurotrachelus caereluscens Singh

Few puparia were collected from underside of rose leaves. Lemon yellow with eyes and abdominal ridge reddish. Takahashi (1932) recorded it from Formosa.

Papillae-like pores on dorsum neither as numerous nor prominent as figured by Singh (1931). Mid-dorsal suture reaching margin, with serrate markings at tip. Some specimens show the operculum covering more than half the orifice.

Host: *Rosa* sp.

Locality: Horticultural gardens, Himayetsagar.

Genus *Trialeurodes* Cockerell

Trialeurodes ricini (Misra)

Though known for long as *Aleyrodes ricini* (nom. nud.) infesting castor, Misra (1923) described it for the first time, retaining the original name. Singh (1931) assigned it to *Trialeurodes* due to the submarginal row of papillae. A *Trialeurodes* is also known from castor in Siam (Reiniking, 1921).

This is widely distributed in all the castor growing regions of the country. In Delhi it is found on perennial castor throughout the year, maximum activity being noticed during May-July. Rao (1942) has worked out its biology at Delhi. It is common on leaves in Hyderabad, though becoming abundant late in the season during the summer months, starting with February. Pupal cases are parasitised by *Encarsia* sp. and preyed on by *Sphaerophora scutellaris* Fab and some coccinellids.

Stray puparia were collected from the other hosts recorded. The specimens do not show submarginal pores prominently.

Hosts: *Ricinus communis*, *Murraya koenigi*, *Rosa* sp., *Euphorbia* sp., *Phyllanthus* sp. (weed)

Locality: Himayetsagar, Bodhan, Warangal, Shamshabad, Jedcherla, Patancheru, Polepalli.

Trialeurodes rara Singh

Singh (1931) records this species in small numbers on *Breynia* sp. Both at Delhi and Hyderabad it is found to infest castor on a scale equal to *T. ricini* (Misra).

Puparia collected at both these places show the following variations from the original description: (i) Caudal margin of vasiform orifice has a distinct cleft. (ii) The number and position of extra submarginal papillae is variable. Few additional papillae are found on the abdominal region. (iii) Some specimens show the mid-dorsum raised into a slight rachis.

Hosts: *Ricinus communis*, *Murraya koenigi*, *Euphorbia* sp.

Locality: Himayetsagar and other places noted under *T. ricini.*

Trialeurodes cotesi (Maskell)

This is one among the first lot of Indian Aleurodidae to be described by Maskell (1895). The original meagre description is supplemented from material collected at Quetta on rose, where it was originally obtained on the same host. The leaves show fairly heavy infestation. Due to presence of submarginal papillae and row of pores it was transferred to *Trialeurodes* from *Aleurodes.*

Puparia brown, elliptic, convex, buried amid copious woolly secretion. After clearing, they turn light brown. Margin deeply crenulate with suture-like lines running a short distance into submargin, which has subelliptical papillae 3–4 deep, except in anterior and posterior regions. Interposed between the margin and the papillae is a row of equally spaced round pores. Three pairs of stout spines, one on either side of mouth parts, second on 3rd thoracic segment, and the last cephalad of the vasiform orifice. Abdominal sutures not very distinct, reaching to subdorsum, forming an imperfect median rachis.

Vasiform orifice subcordate, with inner margin unarmed. Operculum similarly shaped, covering half the orifice. Lingula visible, caudad of operculum, knobbed, setose, and included. A pair of spines at caudal end of case, with another smaller sized pair caudo-laterad.

Host: Rose (Coll: Y. R. Rao).

Locality: Quetta.

Genus *Siphoninus* Silvestri

Siphoninus finitimus Silvestri

Originally described from Italy on Pomegranate by Silvestri, it was first recorded from India by Karam Singh (1931).

This species is found infesting the leaves from December to May. During March and April, when fresh growth occurs, active oviposition is noted. As a result of intense overcrowding by the puparia, the leaves turn yellow. Puparia are parasitised by a chalcidoid. *Chilomenes* is a common predator.

Specimens collected here do not show the caudal corrugation very prominently, agreeing in this respect with Silvestri's original description. Also the caudal two-thirds of the vasiform orifice shows honeycomb sculpturing.

Locality: Himayetsagar.

Host: Pomegranate (*Punica granatum*).

Genus *Bemisia* Q. and B.

Bemisia tabaci (Genn.)

This species was originally described from tobacco plants in Greece by Gennadius in 1889. First to transfer it to *Bemisia*, Silvestri (1934) also was first to synonymise *Bemisia gossipiperda* Misra and Lamba with this species, though the Zoological record (p. 233, 1941) attributes this to Takahashi. Takahashi (1933) however showed that *B. hibisci* described by him was a synonym of *B. tabaci.*

B. tabaci enjoys a cosmopolitan distribution, being found in almost all cotton growing areas. Pruthi and Samuel (1931, 1939, 1941, 1942) record its wide range of host plants in India and have also proved it to be a vector of tobacco leaf curl in North Bihar. It is also a serious pest of cotton in the Punjab. According to Smith (1937) it is the vector of leaf curl of cotton also.

The species is one of the aleurodids known to definitely cause galls. The galls are pinkish eruptions, the puparia being lodged in depressions. The galls are found only on *Achyranthes aspera.*

The puparia, found mostly on the underside of leaves, are small and without any waxy secretion. It is by no means a pest on any of the large number of hosts recorded here, nor does it exhibit any preference to a particular host. Only a few puparia were obtained on each plant.

Hosts: *Altha rosea*, *Gossypium* sp., *Acacia* sp., *Psidium gauyava*, *Hibiscus rosa-sinensis*, *Ficus* sp., *Nicotiana tabacum*, *Dalbergia sisoo Butea frondosa*, *Euphorbia* sp., *Achyranthes aspera*, *Phyllanthus* sp., *Sonchus* sp., *Nyctanthes arbos-tristis.*

Locality: Himayetsagar, Delhi.

Bemisia nigeriensis Corbett

This species was originally described from Nigeria on *Manihot utilissima* and *M. palmata*. It is suspected to be the transmitter of manihot virus, which causes mosaic of cassava (Smith, 1937).

The few specimens collected here are found on both sides of the leaf. There is no marginal secretion, though the dorsum is covered with bloom.

Hosts: *Eugenia* sp., *Moringa pterigosperma.*

Locality: Himayetsagar.

Bemisia leakii (Peal)

Few specimens were obtained at Delhi from *Dalbergia sisoo* from which it was originally described (Peal, 1903).

Genus *Tiawanaleyrodes* Takahashi

Tiawanaleyrodes hexcantha Singh

Puparia small, yellow-white and free of any secretion. About 8–9 per leaf, distributed singly on ventral side.

Median abdominal tubercles with wavy markings, 4 to 6 in number, decreasing in size as they near the vasiform orifice. An additional pair of spines caudo-laterad of the orifice. Granulations along thoracic sutures and near mouth parts. A pair of additional tubercles, smaller than those on 1st pair of legs, present at bases of 2nd pair. The chitinisation of rim of the orifice broken caudad.

Hosts: *Ficus* sp., an unidentified shrub.

Locality: Himayetsagar.

Genus *Aleuromarginatus* Corbett

Aleuromarginatus tephorosiae Corbett

With this species collected on *Tephrosia candida* as type, Corbett (1935) erected the genus.

Puparia found on both sides of leaf show varying shades of brown, with pale-coloured transverse bands on dorsum. No bloom but marginal waxy fringe present. Earlier instars usually on underside.

The presence of the puparia results in pit like depressions on the leaf.

Host: *Tephrosia purpurea.*

Locality: Himayetsagar, Bodhan, Warangal.

Genus *Aleyrodes* Latreille

Aleyrodes schizoukinensis Kuwana

Originally known from Japan, it was recorded for the first time from India by Karam Singh (1931).

Infestation, which is usually heavy, can be easily made out by the abundant bluish, powdery, secretion surrounding the nymphs and puparia, which are exclusively on underside of leaves. Breeding starts in February and March. Eggs laid irregularly. Freshly laid eggs yellow, tipped with black at anterior end. The cases before me show a pair of spines on either side of the mouth parts.

Hosts: *Phyllanthus distichus*, *Phyllanthus* sp.

Locality: Himayetsagar.

Genus *Aleurocanthus* Q. and B.

Aleurocanthus rugosa Singh

Stray specimens were found on *Psidium gauyava* during January at Himayetsagar.

Genus *Aleuroclava* Singh

Aleuroclava complex Singh

With this species as type, Karam Singh (1931) erected the genus.

Third instar nymphs and puparia were obtained during February associated with another undetermined aleurodid on both the hosts recorded here. They are free of any secretion and present on the underside.

Hosts: *Bassia latifolia*, *Aegle marmelos* seedlings.

Locality: Forest nursery, Himayetsagar.

Genus *Aleurolobus* Q. and B.

Aleurolobus barodensis (Maskell)

A common and sometimes serious pest of sugarcane in Hyderabad and some other states like Orissa, Madhya Pradesh, and Bihar. Its incidence is particularly heavy in low-lying plots receiving a poor level of nitrogenous fertilizers (Khan & Rao, 1956).

Host: *Saccharum officinarum*, *Erianthus aurundanaceum*, *E. ciliaris* (?).

Locality: Different localities in Nizamabad Dist.

Genus *Neomaskellia* Q. and B.

Neomaskellia bergii (Signoret)

Infests sugarcane to a small extent. A minor pest.

Host: *Saccharum officinarum*.

Locality: Different localities in Nizamabad Dist.

REFERENCES

Corbett, G. H. 1935. *Ann. Mag. Nat. Hist.*, 10th Ser., 16: 240.
Khan, Md. Quadiruddin, and B. H. K. Rao. 1956. *Ind. Sugar* 6: 267–70.
Maskell, W. M. 1895. *Trans. New Zealand Inst.* 28: 411.
Misra, C. S. 1923. *Proc. Ent. Meeting, Pusa* 5: 130.
Peal, H. W. 1903. *J. Asiat. Soc.*, Bengal 72: 61.
Pruthi, H. S., and C. K. Samuel. 1937. *Ind. Jour. Agri. Sci* 7: 659
Pruthi, H. S., and C. K. Samuel. 1939. *Ind. Jour. Agri. Sci* 9: 223.
Pruthi, H. S., and C. K. Samuel. 1941. *Ind. Jour. Agri. Sci* 11: 387.
Pruthi, H. S., and C. K. Samuel. 1942. *Ind. Jour. Agri. Sci* 12: 35.
Quaintance, A. L., and A. C. Baker. 1913–14. *Bull. U. S. Dept. Agri. Bur. Ent. Tech. Ser.* 27.
Quaintance, A. L., and A. C. Baker. 1917. *Proc. U. S. Nat. Mus.* 51: 335.
Rao, A. S. 1942. Thesis Associateship IARI, New Delhi, p. 19.
Reiniking, 1921. *Phill. Agri.* 9: 185.
Singh, Karam. 1931. *Mem. Dept. Agri. Ent. Ser.* 12.
Singh, Karam. 1932. *Rec. Ind. Mus.* 34: 81.
Singh, Karam. 1933. *Rec. Ind. Mus.* 35: 841.
Singh, Karam. 1938. *Rec. Ind. Mus.* 40: 189.
Singh, Karam. 1940. *Rec. Ind. Mus.* 42: 453.
Smith, K. M. 1937. Text book of plant viruses. London.
Takahashi, R. 1932. *Dept. Agri. Govt. Res. Inst. Formosa* 59: 1.
Takahashi, R. 1933. *Dept. Agri. Govt. Res. Inst. Formosa* 60: 1.
Takahashi, R. 1934. *Dept. Agri. Govt. Res. Inst. Formosa* 63: 39.

Some Interesting Aspects of the World Distribution and Classification of Aquatic and Semiaquatic Hemiptera

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ABSTRACT

This paper corrects some published records on the distribution of certain water bugs, corrections made necessary by the application of modern techniques in the identification of species. It illustrates the distribution of families and genera over the world, genera that are world wide in distribution and genera of the Old World that have counterparts in the New World. It reviews briefly the taxonomic progress of the last forty years and the major problems that face the taxonomists of aquatic Hemiptera today.

My interest in the distribution of the Hemiptera was aroused many years ago by reading an address presented before the Seventh Internatinal Zoological Congress by Dr. Horvath of Budapest. For more than fifty years he was a foremost student of the Hemiptera. In his address he discussed the relation between the hemipterous fauna of Europe and North America. He listed as occurring on both continents, and not artificially imported as are the bed bug and some thirty-eight others, fifty-nine Hemiptera of which eight were water bugs. I found the water bugs to be specifically different, although the superficial appearance justified the misidentifications. How many of the terrestrial Hemiptera recorded as common to the two continents will have to be dropped from the list upon closer study, I do not know. I do know that Dr. Knight has shown that certain mirids, and Dr. Drake that certain saldids are common to Europe and America. I have found two corixids, rare ones, that occur in North America and Europe.[2] The subject needs further study. In the aquatic Hemiptera I am certain it would be erroneous to base conclusions of world distribution, either of genera or species, upon the published records. When I began my studies, *Notonecta undulata* Say, for example, was credited with a distribution extending over the United States and southward to Chile, South America. Examination of thousands of specimens from South America failed to show any specimens of *N. undulata*. The Chilian species proved to be very distinct from it, and it developed that several species were involved in the distributional records of *N. undulata*. According to available records, the genus *Curicta* of the family Nepidae occurs not only in North and South America, but in Australia as well; but the Australian form is not congeneric with the New World *Curicta*.

The same caution must be employed in accepting palaeontological records, for many of them are assigned to wrong genera and in some cases to wrong families. While the palaeontological records are extremely meager and in cases erroneous, a reexamination of such fossils as are available gives us a little background for our understanding of present day distribution.

Without doubt the water bugs were derived from terrestrial forms and have become secondarily adapted to living upon or within the water. Of the fifty-one families of Hemiptera living today seventeen are aquatic or semiaquatic. When these water bugs first invaded the water and became adapted there, we do not know. The first fossil water bugs are from the Jurassic, and these have the general appearance and adaptations of forms living now. There lived in the Jurassic of Europe a giant water bug (Belostomatidae) 50–55 mm. long, the same size and shape of our modern genus *Lethocerus*. (There are no Belostomatidae in Europe today.) There was a Nepa-like form of same size and shape as our present day genus but lacking a respiratory tube; a back swimmer distinctly notonectid in type and a water boatman (Corixidae) 18 mm. long, larger than any corixid living today.

The tertiary fossils include water striders, naucorids, belostomatids, nepids, notonectids and corixids. The *Nepa* found in Baltic Amber and those from the Florissant of Colorado are quite like those of today. One of the corixids from the Florissant, named *Corixa florissentella* by Cockerell, looks like our modern genus *Cymatia. Corixa horvathi* Lomnicki, described from fossils in the Pleistocene Ozocerite Clay from southern Poland, is very near in all its characters, even to the claspers of the male genitalia, to *Arctocorisa carinata* (Sahlb.) and *A. germari* (Fieber), alpine species living today, and *Corisa ozokeritica* Lomnicki from the same clays is very close to *Callicorixa praeusta* (Fieber), a boreal living species. So that we are justified in concluding that the Lower Pleistocene Corixidae fauna of southeastern Poland had a boreal aspect.

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[1] Contribution No. 952 of the Department of Entomology, University of Kansas, Lawrence. This paper was prepared with the aid of a grant from the National Science Foundation.

[2] *Glaenocorisa quadrata* Walley in Alaska, Quebec, Newfoundland, and Norway; *Sigara (Subsigara) fallenoidea* Hungfd. in Canada and Ireland. The circumpolar genus *Callicorixa* has no species common to Europe and America, but the subspecies *Callicorixa producta noorvikensis* Hungfd. is found in east Asia, Alaska, and Canada, and *Trichacorixa reticulata* (G-M), which is common in North and South America, has been reported from Hawaii, the Philippines, and China. Dr. Todd, 1955, reports that the gelastocorid *Nerthra rugosa* (Desj.), which was described from the island of Mauritius, occurs also in Florida and Panama.

In approaching our problem of present day distribution, we must bear in mind that many of our water bug genera have existed unchanged for 50 million years or more and that some species have persisted for millions of years. Indeed there are species of insects in the Baltic amber (45 million years old) that are very near if not identical with species living today. The evolution of the water bugs was ably discussed by Dr. China in the Symposium of Organic Evolution at New Delhi, India, in 1953.

In the living families of Hemiptera we can find a biological sequence showing a gradual change from littoral life to truly aquatic existance. From the Heteroptera, Dr. China[3] figures the semiaquatic Hemiptera (Amphibicorisae) as arising from the Proto-Saldidae and the Aquatic Hemiptera (Hydrocorisae) from the Proto-Ochteridae. Coming from the ancestors of the rapidly running and flying Saldidae with their long antennae, we have the semiaquatics, and from the ancestors of the Ochteridae with their short antennae that also live along the shore, we derive the aquatics. A step closer to aquatic life are the more sluggish toad bugs (Gelastocoridae) with their habit of burrowing in the mud. They have hidden antennae, raptorial fore legs, and short beaks. The Naucoridae or creeping water bugs may be our oldest living true aquatics, and from their ancestors, the Proto-Naucoridae, arose also the other families. Water bugs are, among insects, unusually valuable for the study of natural distribution because they are not likely to be transported by the agencies of man.

With the exception of the marine Aepophilidae, all the families of water bugs are mainly fresh water forms. In the family Gerridae we find the pelagic genus *Halobates*, which lives upon the surface of the oceans sometimes a thousand miles from land. In other families we find now and then a species that can survive in saline waters.

In the Corixidae we have the New World genus *Trichocorixa*; some species of this genus inhabit tidal pools of brackish water and saline springs as well as fresh water ponds and pools. In 1937 Dr. Beamer found a *Trichocorixa* species (*T. verticalis interiorei* Sailer) in salt water pools in Manitoba, Canada. He was not equipped to make a quantative analysis of the water but reported that this species was the only one living in the pool, and it was there in numbers. Other bugs that flew into the pool died there.

Of the seventeen families that have an ecological association with the water:

I. Some may live upon the shore as do the Saldidae, Ochteridae and Gelastocoridae.

II. Others may live at the water's edge, running out upon the water when disturbed, often on rafts of floating vegetation like the Mesoveliidae, Hebridae, Hydrometridae, and Veleidae.

III. Still others may course the surface film with the greatest of ease as *Gerris* on quiet waters, *Rhagovelia* on rapid waters, and *Halobates* far out at sea.

IV. While still others live subaquatic lives: By clinging to supports and resting in contact with the surface as the Belostomatidae do with their short retractile tube or as the Nepidae do with their long respiratory tube.

By clinging to submerged vegetation or as bottom dwellers making excursions to the surface for air as do the Naucoridae and Corixidae, or as free swimmers like the backswimming Notonectedae, Pleidae, and Helotrephidae that also come to the surface to renew their air supply. Many of these also cling to submerged supports.

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[3] The Evolution of the Water Bugs, by W. E. China. Bulletin No. VII. Symposium on Organic Evolution. National Institute of Sciences of India, New Delhi.

A complete mapping of the geographical distribution of all the semiaquatic and aquatic Hemiptera is not possible at this time. There is too much territory unexplored and too little known about the taxonomy in some of the families. Nevertheless it is profitable to summarize our present knowledge in some of these families.

The SALDIDAE or shore bug family has been neglected since Reuter's day until recent years. In 1950 Carl J. Drake and Ludvik Hoberlandt published their catalogue of genera and species of Saldidae in *Acta Entomologica Musei Nationalis Pragae*, Vol. 26, No. 376. This is an interesting contribution. Of the fourteen genera that they recognize, only two, *Ioscytus* and *Lampracanthia*, are confined to North America, and two, *Orthophrys* and *Omania*, to Africa. To the genus *Pentacora*, which we thought was confined to the New World, they have added a species from west Australia and another from Celebes. The curious genus *Saldoida* has two species in the United States and two species in the Orient (Formosa and the Philippines). Eight other genera are common to both hemispheres, with ten or more species credited with occurring in both the Old and New worlds. The variable and wide ranging *S. pallipes* (Fabr.) is recorded from Asia, Europe, and Africa in the Eastern Hemisphere and from Canada southward through central and insular America to Chile and Brasil in the Western Hemisphere. A new key to genera and species is much to be desired in this family.

The GELASTOCORIDAE, or toad bug family, received a taxonomic revision in 1955 by Edward L. Todd in *University of Kansas Science Bulletin*, Vol. 37, Pt. 1, pp 277–475. The family contains two genera. The genus *Gelostocoris* Kirkaldy 1897 is confined to the New World and contains thirteen species, while the genus *Nerthra* Say 1832, better known as *Mononyx* Laporte 1833, contains sixty-one species. Australia has fourteen species, Tasmania two, Solomon Islands four, and New Guinea five. The genus is represented by a single species on Guam, in the Philippines, and in Sumatra. In Asia there is one species in China, two in India, one in Assam, and one in Nepal. Some of the above of course are duplications. Africa has one widespread species. The New World has thirty-two species, only three of which appear in the United States, the others are scattered from Mexico (with seven) through Central America to Chile, the Argentine, and Brazil. There are ten species recorded in Brazil.

The PELOGONIIDAE, better known as Ochteridae, might be called the velvety shore bugs. They seem to be intermediate between the Saldidae, which have exposed antennae, and the Gelastocoridae which have hidden antennae. It is a small family containing three genera. The genus *Megochterus* Jaczewski 1934 is represented by *M. nasutus* (Mont.) in Australia; the genus *Ocyochterus* Drake and Gomez-Memor 1954 by *O. victor* (Bolivar) in South America; and the type genus *Pelogonus* Latra. 1809 or *Ochterus* Latr. 1807, which contains only a few species but which is represented from Australia and northward to Japan and westward from Cochin-China to southern France and Africa by perhaps five Old World species and by fourteen species in the New World. In 1943 Dorothydean Schell published "The Ochteridae of the Western Hemisphere" in the *Journal of the Kansas Entomological Society*, Vol. 16, pp. 29–47, and in 1934 T. Jaczewski published "Notes on the Old World Species of Ochteridae" in the *Annals and Magazine of Natural History*, Ser. 10, Vol. 13, pp. 597–613.

The CORIXIDAE are called water boatmen in America. These unique insects have always been a taxonomic puzzle. While considered Hemiptera, they do not have the characteristic segmented beak of Hemiptera. They scoop up the organic ooze with the palae of the front legs and ingest solid food. They can remove the chlorophyll from coarse filamentous algae or pack their stomachs with skeins of filamentous algae. While some, like *Cymatia*, may be largely predaceous and others on occasion may capture animal food, their unfailing supply of food is plant material, which makes them the dominant family of water bugs.

Living in the water and being streamlined to a common plan, they have been a difficult group taxonomically. It was thirty years before I could publish the Corixidae of the Western Hemisphere[4], and I am still working on the Old World Corixidae.

Numerous distributional maps are available for the Corixidae of the Western Hemisphere, which now includes some 212 species and 12 subspecies. Of the 23 genera represented, only five are found also in the Old World, which has in addition nine genera not found in the Americas.

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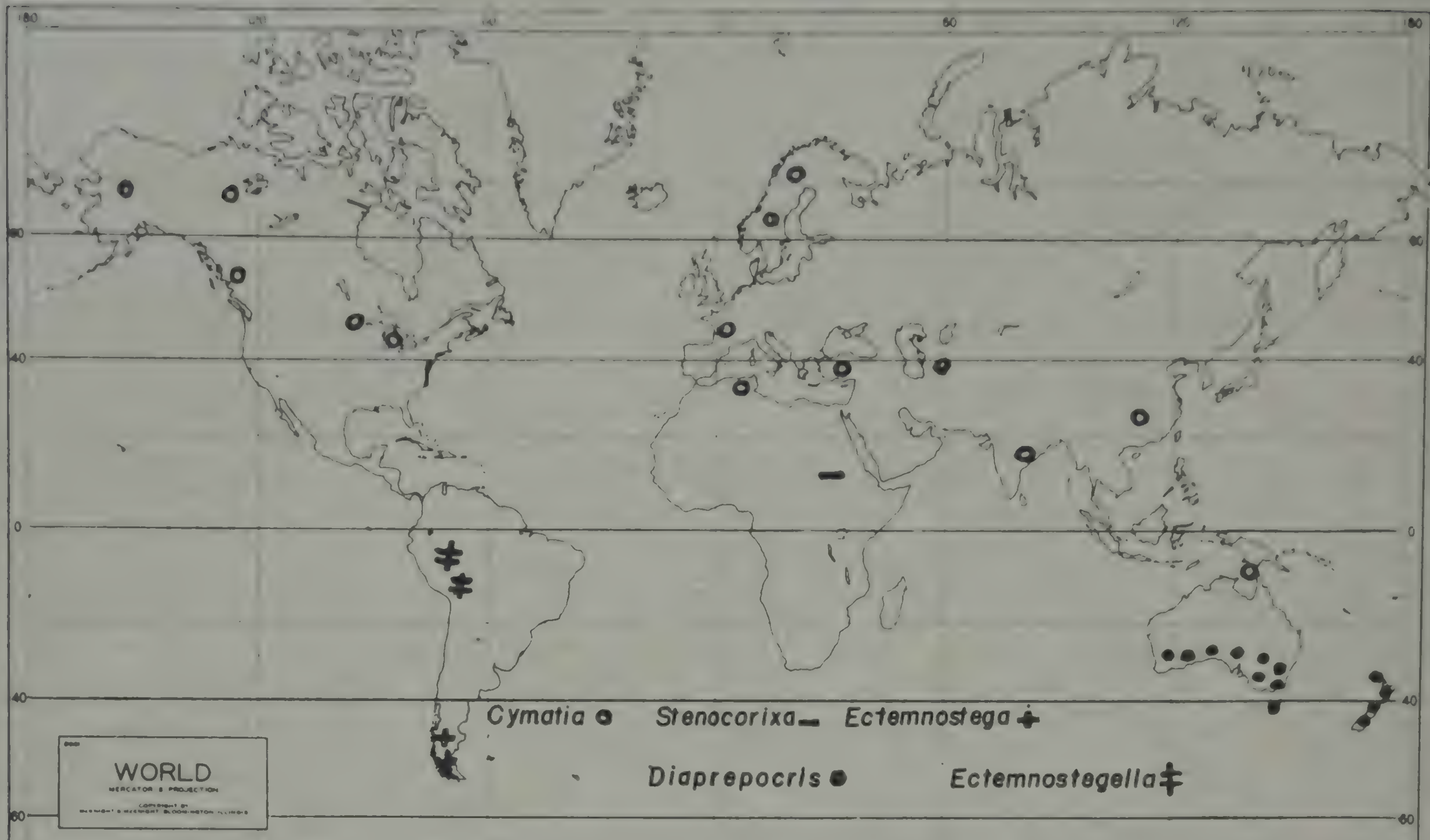
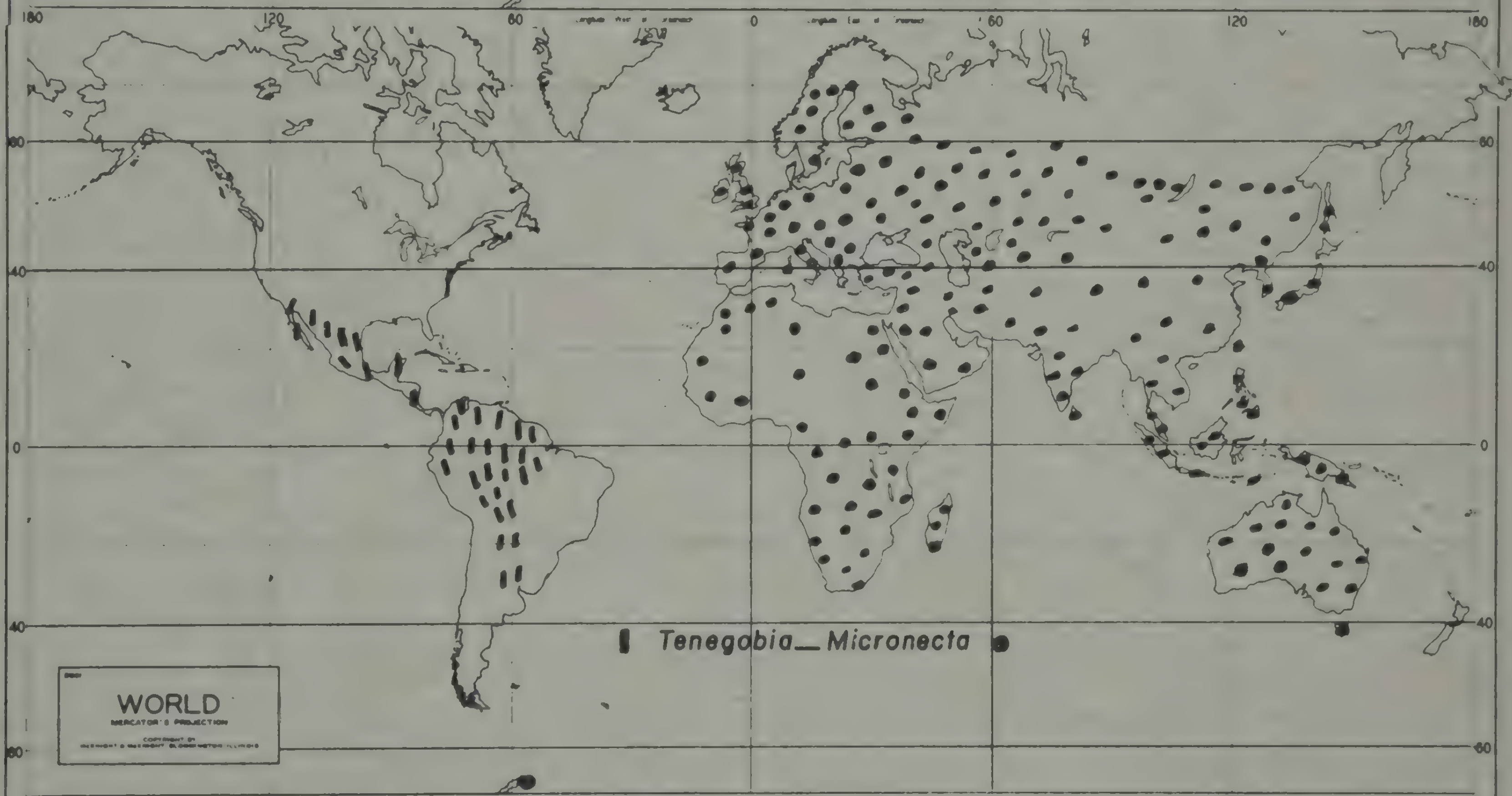
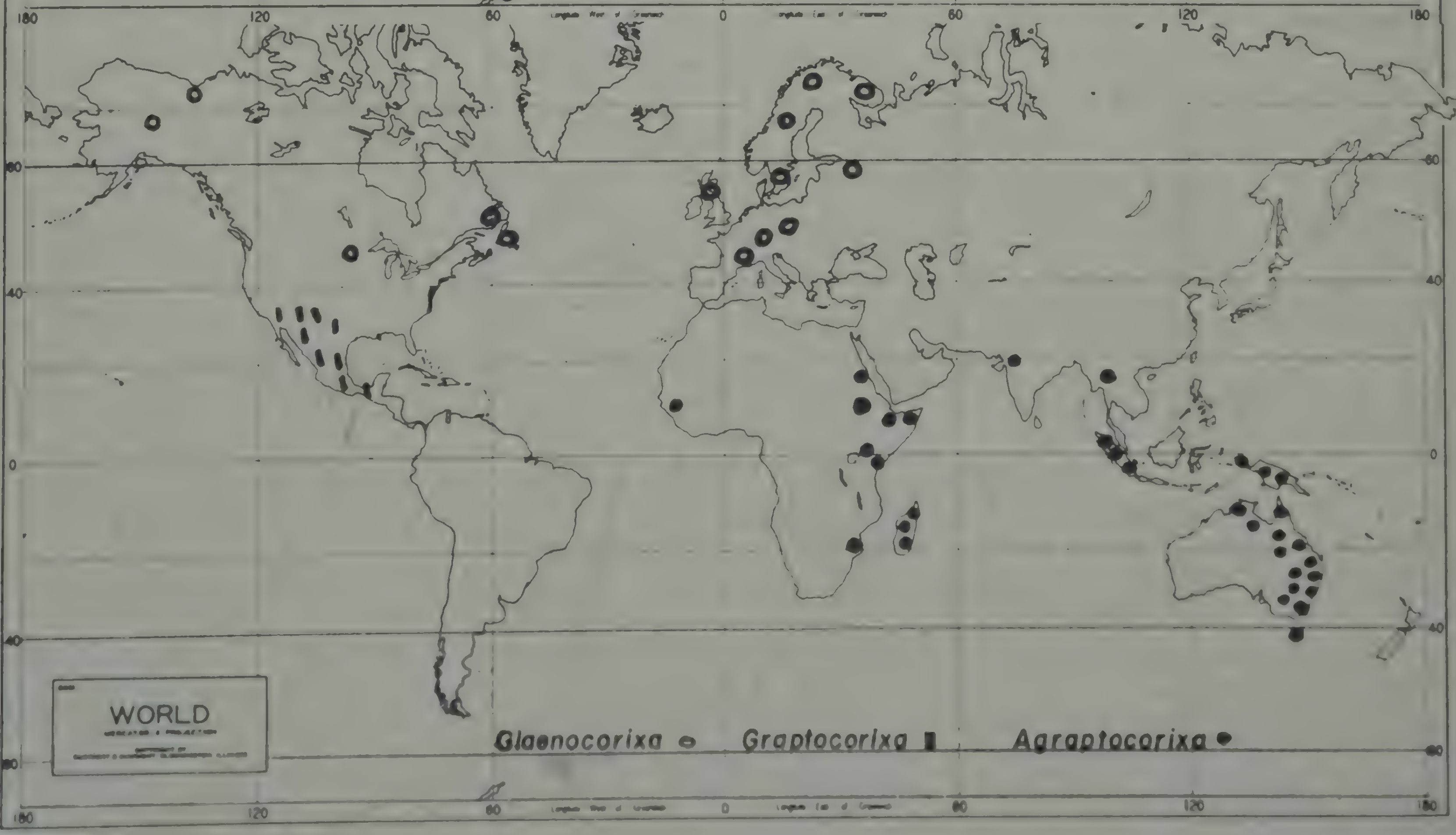
[4] *University of Kansas Science Bulletin*, Vol. 32, pp. 1–827, 1948.


WORLD
MERCATOR'S PROJECTION
Cymatia ○
Stenocorixa ▬
Ectemnostega ✚
Diaprepocris ●
Ectemnostegella ‡
180
120
60
0
60
120
180
60
40
0
40
60


WORLD
MERCATOR'S PROJECTION
Tenegobia ▮
Micronecta ●
180
120
60
0
60
120
180
60
40
0
40
60


WORLD
MERCATOR'S PROJECTION
Glaenocorixa ○
Graptocorixa ▮
Agraptocorixa ●
180
120
60
0
60
120
180
60
40
0
40
60

While there has developed in South America the curious subfamily Heterocorixinae with 13 species and in southwestern North America the Corixinae tribe Graptocorixini with 16 species in two genera, we find our most primative and interesting subfamily of Corixidae in Australia and New Zealand. In these Diaprepocorinae the scutellum is large and exposed, and they possess ocelli that are lacking in all other species of the family (see Fig. 1). In the African Sudan there is a strange looking spotted species with a narrow interocular space, elongate body, and so little asymmetry in the male abdomen that the sexes are difficult to distinguish. What its relatives may have been I do not know. It is *Stenocorixa protrusa* Horvath, and it stands alone as a representative of a strange subfamily (see Fig. 1). On this same plate is figured the distribution of the genus of *Cymatia*. There is one species in North America and six species in the Old World. In Europe there are three species, two of which reach North Africa. In Asia there is one species from Turkestan and one in China and India. Recently I described one from an island between New Guinea and Australia, the first species recorded for the southern hemisphere.

The subfamily Micronectinae comprises very small to minute corixids that have an exposed scutellum. It is represented in the Western Hemisphere by the genus *Tenegobia* with seventeen species, all south of Mexico except one, and in the Eastern Hemisphere by *Micronecta* with more than one hundred species. (see Fig. 1).

Most Corixidae have males that are dextral in the abdominal asymmetry, but two genera have sinistral males. These are *Corixa*, which are large corixids (seven species) occurring in Europe, Canary Islands, North Africa, and east to India, and *Trichocorixa*, which contains small species found in North and South America.

The *Trichocorixa* are tolerant of brackish water. Dr. Williams found *T. recticulata* in tidal pools in Hawaii. This species turned up in China and was identified by Dr. Lundblad. I have found it in a collection of insects from the Philippines. The species is common in Mexico and California.

One interesting record of distribution of *Trichocorixa* came to my attention nearly 30 years ago. No corixid species had ever been found in Bermuda. Then in 1927 a hurricane swept across the Greater Antilles, Cuba, and Puerto Rico and spent itself at Bermuda. It happened that Mr. L. Ogilvie of the Bermuda Agricultural Station, who had devoted considerable time to a survey of the water insects of Bermuda, was sitting in his yard when a considerable number of Corixidae dropped out of the air into a tub of water in his yard. He knew the presence of these water bugs was new to Bermuda and sent them to me for determination. The species proved to be *T. verticalis verticalis*, one that is common enough in Cuba and must have been delivered these 1200 miles away by the force of the storm.

Fig. 1 shows the genus *Glaenocorixa*, which is a small northern genus found in North America and Europe, and the genus *Graptocorixa*, which is Sonoran and confined to southern California, Arizona, New Mexico, and Mexico. (Several other genera of Corixidae have roughly the same distribution, and in the Belostomatidae, *Abedus* has identically the same range). The genus *Agraptocorixa* is found in Africa and eastward to Australia.

Fig. 2 is given to show the distribution of the two species of *Centrocorisa* that were so long confused. The circle represents *C. nigripennis* (Fabr.), which has been taken in Texas, and the circle with a dot is *C. kollarii* (Fieb.). Shown also are *Morphocorixa*, with three species and *Neosigara*, with three species in Colombia, Ecuador, and Peru. *Pseudocorixa*, with five species, extends from Arizona to Guatemala. In the Old World *Heliocorisa* has a single species. *Hesperocorixa* crosses North America and extends from Japan to England and Algeria. The genus *Sigara* is widespread over the world and contains many subgenera. The map shows that the subgenus *Tropocorixa* goes straight across the southern hemisphere.

The Notonectidae of the world have been fairly well studied taxonomically. We have the following papers: "The Genus *Notonecta* of the World", by H. B. Hungerford, *University of Kansas Science Bulletin*, Vol. 34, pp. 5–195, Plates I to XVII (five in color) 1933; "A Study of the Genus *Martarega*," by Fred S. Truxal, *Journal of the Kansas Entomological Society*, Vol. 22, pp. 1–24, Plates I–V, 1949; "A Revision of the Genus *Anisops*",

←— Fig. 1. Distribution of genera of Corixidae.

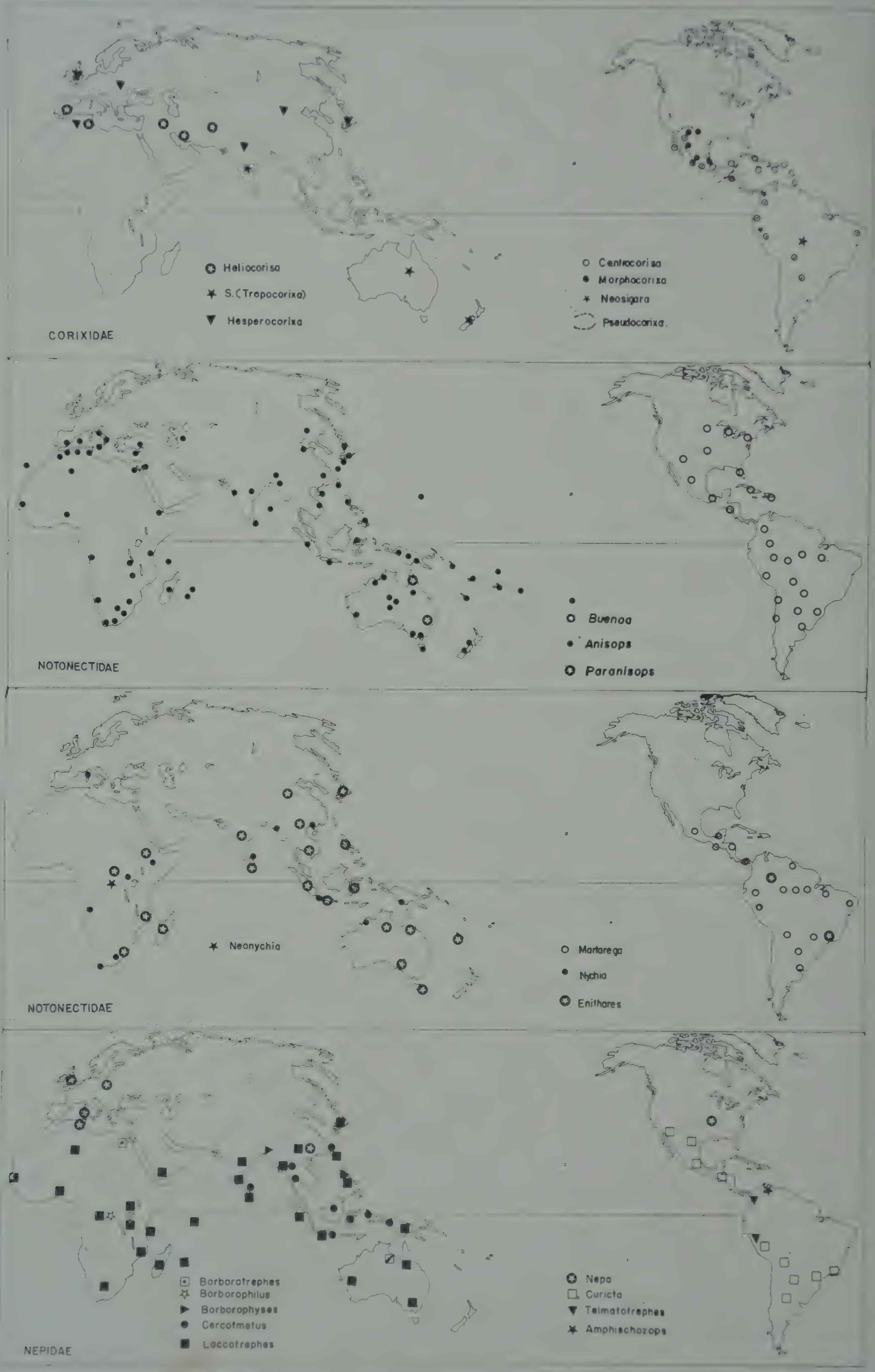

Heliocorisa
S. (Tropocorixa)
Hesperocorixa
CORIXIDAE
Centrocorisa
Morphocorixa
Neosigara
Pseudocorixa.
Buenoa
Anisops
Paranisops
NOTONECTIDAE
Neonychia
Martarega
Nychia
Enithares
NOTONECTIDAE
Borborotrephes
Borborophilus
Borborophyses
Cercotmetus
Laccotrephes
Nepa
Curicta
Telmatotrephes
Amphischozops
NEPIDAE

Fig. 2. Distribution of genera of Corixidae, Notonectidae and Nepidae. [S. (*Tropocorixa*) also occurs in south central Africa].

by George T. Brooks, *University of Kansas Science Bulletin*, Vol. 34, Pt. 1, pp. 301–519, Plates XXXVI–LVII, 1951; "A Revision of the Genus *Buenoa*", by Fred S. Truxal, *University of Kansas Science Bulletin*, Vol. 35, Pt. 2, pp. 1351–1532, Plates CI–CXVII. 1953. A study of the genus *Enithares* by George T. Brooks is awaiting publication. Keys for the identification of species are available in all genera. The subfamily Anisopinae includes the genera *Buenoa*, *Anisops* and *Paranisops* (See Fig. 2). *Buenoa* occupies the New World, *Anisops* the Old World, and *Paranisops* is found only in Australia. The first two genera place their eggs in plant tissue and have their front and middle legs fashioned to serve as a plankton crib for the capture of food. They are the only known aquatic Hemiptera that can maintain hydrostatic balance in the water, and they are the only ones with large quantities of oxyhaemoglobin tissue. I suspect it has something to do with maintaining hydrostatic balance for, of all the water bugs, only *Buenoa* and *Anisops* can cruise submerged with slight effort. *Buenoa* has forty-one species in the Americas. *Anisops* has ninety-five species in the Old World and ranges from the Fiji Islands in the Pacific across Australia and eastern and southern Asia, to Africa and the Canary Islands. Similar insects occur as fossils from the Tertiary. *Paranisops* seems to be a connecting link between *Anisops* and *Notonecta.*

In Fig. 2 it will be noted that the genus *Enithares* has only two species in South America; the other forty-two species are scattered from Africa and across south and east Asia to Australia and beyond. The tribe Nychini has three genera. The genus *Nychia* is widespread in the Old World, but whether it contains only one or three or four species is not clear. Its counterpart in the New World is *Martarega*, and it contains eleven species, all of them south of the middle of Mexico. *Neonychia congoensis* (Hungerford) in Africa stands alone.

The genus *Notonecta* occurs on all the continents. It has been divided into five subgenera. The subgenus *Notonecta* has two representatives in eastern North America and a dozen species in the Old World. This is the only subgenus represented in Canary Islands, North Africa, and Europe, and it extends eastward across India to east China. The subgenus *Paranecta* is the common one in North and South America. However, there is only one species in west and south Africa and six up the east coast of Asia. The subgenus *Erythronecta* extends from southern California and Arizona southward across Mexico to Costa Rica, and the subgenus *Bichromonecta* occupies the same territory plus an extension into Colombia, S. A. The subgenus *Enitharonecta* is represented by a single species in West Australia.

The NEPIDAE: On Fig. 2 is the geographical picture of the genera of the water scorpions. In this well known family the genus *Ranatra* is found on all the continents and some of the islands, so I have omitted it from the map. *Nepa* is a small genus with one species in North America and a few elsewhere. There are two in all of Europe and Algeria and another in China. The other eight genera are confined either to the Western or Eastern Hemisphere. For example, *Curicta* of the New World is replaced by *Laccotrephes* in the Old World (the Australian *Curicta augusta* Hale is not a *Curicta*). *Cercotmetus* is largely East Indian in distribution. *Nepella* is represented by a single species in Africa.

Dr. Jose DeCarlo has been the most active recent student of these insects in the Western Hemisphere. He places *Ranatra* and its relatives in a separate family, the Ranatridae. Two of his major contributions are the following: "Nepidos de America", *Revista del Instituto Nacional de Investigacion de las Ciencias Naturales, Ciencias Zoologicas*, Tome I, No. 9, pp. 385–421, 1951 and "Los Ranatridae de Sud America", *Anales del Museo Argentino de Ciencias Naturales*, Tome 42, pp. 1–38, Plates I–VII, 1946.

For North American species it is still necessary to use my "Nepidae of North America", *Kansas University Science Bulletin*, Vol. 14, pp. 425–469. Plates XLIV–LI. 1922, which needs revision.

The determination of Old World species requires the knowledge of many authors, from early days to Lundblad, Esaki, and Poisson.

In "Zur Kenutnis der aquatilen und semiaquatilen Hemipteren von Sumatra, Java and Bali," *Archiv für Hydrobiologie*, 1933, Suppl., Bd. 12, Tropische Binnengewasser IV seute 1–194, 263-489, 1933, Dr. O. Lundblad has given the most complete and satisfying faunal report I have seen. Here you will find lists of species and in many cases keys for

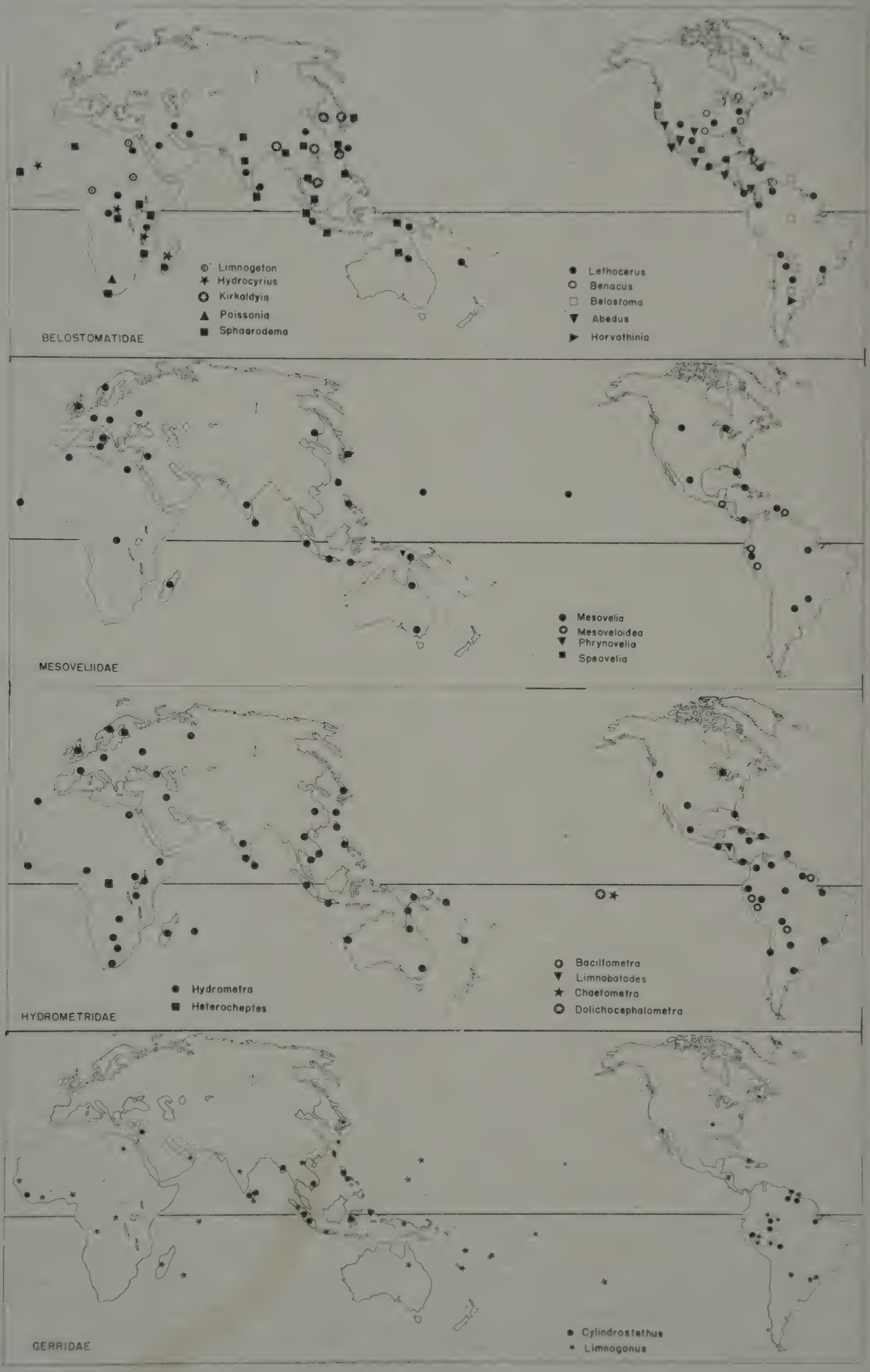

◎ Limnogeton
✶ Hydrocyrius
✪ Kirkaldyia
▲ Poissonia
■ Sphaerodema
BELOSTOMATIDAE
● Lethocerus
○ Benacus
□ Belostoma
▼ Abedus
▶ Horvathinia
● Mesovelia
○ Mesoveloidea
▼ Phrynovelia
■ Speovelia
MESOVELIIDAE
● Hydrometra
■ Heterocheptes
HYDROMETRIDAE
○ Bacillometra
▼ Limnobatodes
★ Chaetometra
✪ Dolichocephalometra
GERRIDAE
● Cylindrostethus
* Limnogonus

Fig. 3. Distribution of genera of Belostomatidae, Mesoveliidae, Hydrometridae and Gerridae.

identification. He also separates the Nepidae and Ranatridae and gives a key to the species of Ranatridae.

The Belostomatidae: This family contains our largest water bugs. Those belonging to the genera *Lethocerus*, *Benacus*, *Kirkaldyia* and *Hydrocyrius* are often called "Giant water bugs" or "Electric light bugs," and in some places have been used as food. Only *Lethocerus* is cosmopolitan in distribution. It and *Benacus* are the only two I know for sure that do not lay their eggs on the back of the males. I do not know about *Kirkaldyia*, but I have specimens of the large *Hydrocyrius* from Madagascar, *Limnogeton* from Africa, *Sphaerodema* in the Old World, and *Abedus* and *Belostoma*, which replace it in the New World, with males carrying eggs. Note the absence of the family in Europe (see Fig. 3). Yet in Jurassic times there were giant water bugs there. Note the distribution of *Abedus* and *Benacus* in the New World and of *Kirkaldyia*, *Limnogeton*, and *Hydrocyrius* in the Old World.

Here again it is easier to identify Western Hemisphere species. Dr. Jose De Carlo has given us the following: "Los Belostomidos Americanos", *Anales del Museo Argentino de Ciencias Naturales*, Tome 39, pp. 189–260, Plates I–VIII, 1938 (this he is revising), and "Revision del Genero *Abedus* Stäl", *Comunicaciones del Museo Argentino de Ciencias Naturales*, "*Bernardino Rivadaria*" *serie Ciencias Zoologicas* No. 5, pp. I–IX, 1–24, Tab. I–III. "The Giant Water Bugs" by Carl Cummings, *University of Kansas Science Bulletin*, Vol. 24, pp. 197–219, Plates XVIII–XIX, 1933, is still useful as is Jose Hidalgo's "The Genus *Abedus*", *University of Kansas Science Bulletin*, Vol. 22, pp. 493–519, 1935. For the Old World we must know the literature. The most recent key seems to be E. S. Brown's key to *Hydrocyrius* in *Proceedings of the Royal Entomological Society of London*, Ser. B, Vol. 17, pp. 109–114, 1 Plate, 1948. See also the Lundblad reference above for help on species from the Far East.

The Naucoridae, or creeping water bugs, needs taxonomic attention. The Western Hemisphere forms are under study by Dr. Robert L. Usinger in California and his student Dr. Ira LaRivers in Nevada. Dr. Usinger's "Key to the Subfamilies of Naucoridae, with a Generic Synopsis of the New Subfamily Ambrysinae", *Annals of the Entomological Society of America*, Vol. 34, pp. 5–15, 1941 was a good start. This he has followed with several other useful papers, including "Classification of the Cryphocricinae" in *Annals of the Entomological Society of America*, Vol. 11, pp. 329–343. Dr. LaRivers, besides several other papers, has given us "The *Ambrysus* of Mexico", *University of Kansas Science Bulletin*, Vol. 35, Pt. II, pp. 1279–1349, Plates XCV–C, 1953, and "A Revision of the Genus *Ambrysus* in the United States", *University of California Publications in Entomology*, Vol. 8, No. 7, pp. 277–338, Plates I–IV, 1951. Dr. DeCarlo has worked on South American forms. For the Old World we have Dr. Poisson reporting on African species and Dr. Lundblad for the Far East (see reference above). Of the thirty-two genera in my catalogue, I feel a pressing need for a key to *Pelocoris*. I have not mapped the distribution of genera but feel that the discovery of the subfamily Potamocorinae in South America should stimulate further collecting there.

Mesoveliidae: This family of small striders has a wide distribution as shown on the chart. It is represented by nine species in the Western Hemisphere (eight *Mesovelia*, one *Mesoveloidea*) and by thirteen or fourteen species in the Eastern Hemisphere (eleven-twelve *Mesovelia*, one *Phrynovelia*, one *Speovelia*). It is interesting to note the wide distribution of certain species (see Fig. 3). In the New World, *M. mulsanti* B. White extends from southern Canada through the Carribean Islands to the Argentine and to Hawaii. In the Old World, *M. furcata* M. & R. extends from Siberia to Norway and south through Europe to North Africa; *M. vittigera* Horvath from France to Egypt, Algeria, Palistine, Senegal, Belgian Congo, and Madagascar; while a very near relative *M. orientalis* Kirk. is found in Ceylon, Sumatra, Java, Lombok, Philippines, Formosa, New Guinea, and Guam. Moreover *M. pacifica* Usinger from Guam has a very close relative in *M. horvathi* Lund. in Sumatra and Java. For a key to species of the Far East see Lundblad, (reference above) and add *Mesovelia hackeri* Drake 1941.

The Hebridae: This family of small striders is easily recognized, and the genus *Hebrus* is widespread. There are six genera, the best known being *Hebrus* with five-segmented antennae and *Merragata* with four-segmented antennae. These two are widely distributed. Dr. Raymond Poisson in *Ann. Mus. Congo Tervuren*, in 4° Zool., 1954, Miscellanea

Zoologica, H. Schouteden, p. 509, gives a world map showing *Merragata* to occur in Hawaii, North and South America, and in the Canary Islands. Then it is absent in Africa and eastward until India is nearly passed. It occurs in Java and Australia. On the other hand Dr. Poisson has described a number of species of *Hebrus* from Africa and records Madagascar also. Therefore *Hebrus* is present in many places lacking *Merragata*. Of the remaining genera, there is *Lipogomphus* in South America and three genera in the Orient.

For the Western Hemisphere there is "Notas Sobre Hebridae del Hemisferio occidental", by C. J. Drake and H. M. Harris, *Notas del Museo de la Platta*, Tome 8, Zoologia, No. 64, pp. 39–58, 1943. For the Eastern Hemisphere, there is no one general paper. Europe is covered by a number of works, the latest of which is by Wolfgang Stichel: "Illustrierte Bestimmungstabellen der Wanzen II, Europa." For the African species Dr. Raymond Poisson's numerous papers are absolutely necessary, and for the Far East see Lundblad, p. 263. (see reference above).

HYDROMETRIDAE: Among these slender little "marsh treaders" the genus *Hydrometra* has a wide distribution with thirty-six species in the Western Hemisphere and perhaps fifty-eight in the Old World (see Fig. 3). Of the other five genera, all are monotypic and restricted to a single location except *Bacillometra* of South America, with its four species. The only paper covering the Hydrometridae of the world is the paper entitled "The Hydrometridae of the Hungarian National Museum and Other Studies in the Family", by H. B. Hungerford and N. E. Evans in *Annales Musei Nationalis Hungarici*, Vol. 28, pp. 31–112, Plates I–XII, 1934. Since then Poisson, Hoberlandt, Drake, and I have described species, and China and Usinger have given a key to the subfamilies and genera of Hydrometridae of the world in *Rev. Zool. Bot. Africa*, Vol. 41, pp. 314–319, 1949.

GERRIDAE: The family Gerridae contains some forty-seven genera arranged at present in four subfamilies (Gerrinae, ten genera; Ptilomerinae, ten; Halobatinae, twenty-five; and Rhagadotarsinae two genera.)

In the subfamily Gerrinae, only three genera are common to the Old and New Worlds. These are *Gerris*, *Limnogonus*, and *Cylindrostethus*. *Gerris* is widespread, while the other two show a pattern distribution, particularly in the Western Hemisphere (see Fig. 3).

Cylindrostethus. This genus of rather large water striders is readily recognized by a unique appearance that they all share and by having scent gland channels leading from the omphalium and ending laterally in front of the hind acetabula beneath a tuft of hairs. In the New World there are seven species confined to South America, and in the Old World there is one in Africa, one in the Jordan Valley, and others eastward from Ceylon to the Philippines.

Limnogonus. Of the fourteen species of New World *Limnogonus*, ten are from South America, and only two reach north into southern United States. (*L. hesione* Kirk., Ohio and southeast to Florida and Cuba; and *L. franciscanus* Stål, into southern Texas and southern California). In the Old World there are species in Africa, Madagascar, and eastward through the East Indies, India, China, Australia, and islands of the Pacific, and some species are widely distributed. For example *L. fossarum* occurs in India, China and bordering islands, Formosa, and Philippines around to Sumatra, and Dr. Usinger reports it from Guam along with two other species of the genus.

Tenagogonus–Limnometra Complex (see Fig. 4). The genera of Gerridae are undergoing revisional study. For example the *Tenagogonus* Stål-*Limnometra* Mayr complex has been a problem and Dr. Bergroth after some hesitation placed these genera together, but Lundblad (1934) revived *Limnometra*, and I agree with him. However, the new world species we have been assigning to *Tenagogonus* are not congeneric with the above complex, but in general facies look more like *Limnometra*.

The New World contributes *Potamobates* and an unnamed genus now masquerading under the name of an Old World genus (*Tenagogonus*). The Old World supplies six genera, all of them with representatives in India.

The subfamily Ptilomerinae is confined to the Old World. One genus occurs in Madagascar, and others occur from Turkestan, India, Sumatra, and the Malay Peninsula to Formosa (Taiwan). The subfamily Halobatinae is widespread. Nine genera are New World, and sixteen are Old World genera. Of the nine New World genera only two have

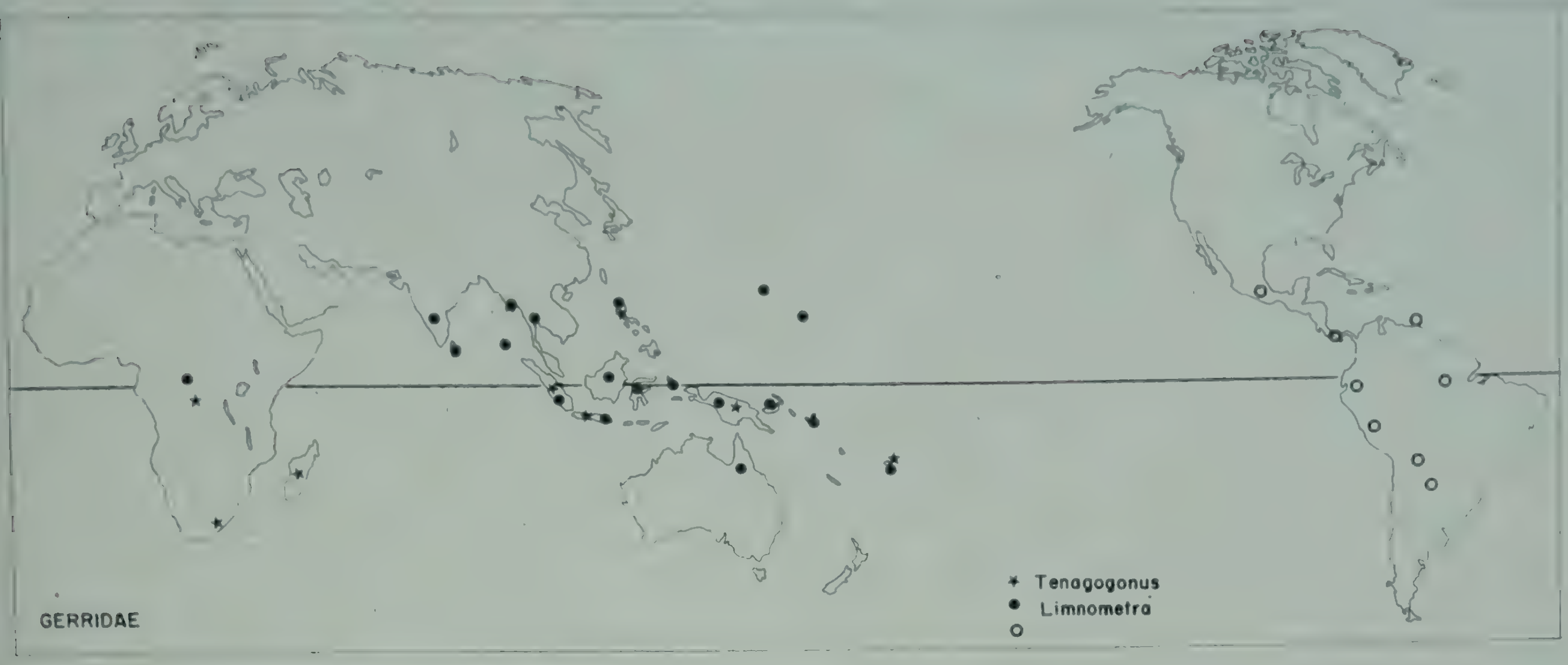


Fig. 4. Distribution of genera of Gerridae. (The open circles indicate the genus *Tachygerris.*)

representatives in the United States, others are in Mexico and from the West Indies to Brazil, South America. Of the Old World genera, four are confined to Africa, and one (*Metrocoris*) ranges eastward to India and China. The others occur in India, East Indies, and Japan, and one genus (*Hermatobates haddonii* Carpenter) has been reported from the Marquesas and New Caledonia, Torres Straits, Philippine Islands, and some other places.

The subfamily Rhagadotarsinae is represented in the Western hemisphere by twenty-four species of Rheumatabates, and in the eastern hemisphere by two species of *Rhagadotarsus*, one in Africa and one described from Formosa but found also in Sumatra, Java, the Philippines, China, and India.

The literature is voluminous and widely scattered. For the Western Hemisphere, the Gerrinae may be identified by "The Gerrinae of the Western Hemisphere", by C. J. Drake and H. M. Harris, *Annals of the Carnegie Museum*, Vol. 23, pp. 179–240, pp. XXI–XXVI, 1934, and by "The Rhagadotarsinae by The Genus *Rheumatobates*", by H. B. Hungerford, *University of Kansas Science Bulletin*, Vol. 36, Pt. 1, No. 7, pp. 529–588, Plates VII–XIV. 1954; The Halobatinae by various papers, including "A Monograph of the Genus *Metrobates*", by L. D. Anderson, *University of Kansas Science Bulletin*, Vol. 20, No. 16, pp. 297–311, Plate XXV, 1932, and "A Synopsis of the Genus *Metrobates*", by C. J. Drake and H. M. Harris, *Annals of the Carnegie Museum*, Vol. 21, No. 2, pp. 83–88, Plate 11, 1932.

A survey of the species of *Trepobates* was published by C. J. Drake and H. M. Harris in *Bull. Brooklyn Entomological Soc.*, Vol. 27, No. 2., pp. 113–123, 1932. See also "The Genus *Telmatometra*", by Eugene Kenaga, *Univeristy of Kansas Science Bulletin*, Vol. 27, No. 9, pp. 169–183, Plate XLL. (key to subfamily Halobatinae); "A Study of the Genus *Brachymetra*", by J. Gilbert Shaw, *University of Kansas Science Bulletin*, Vol. 21, No. 9, pp. 221–233, Plate XX, 1933; "A Key to *Platygerris*", by H. B. Hungerford, *Bull. Brooklyn Entomological Soc.*, Vol. 27, pp. 178–182, 1932. There is more to be done before the Halobatinae of the Western Hemisphere are easily identified. For the Eastern Hemisphere one needs numerous papers by Raymond Poisson, Teiso Esaki, and others. "The Subfamily Ptilomerinae", by Esaki in "*Eos*" *Revista Espanola de Entomologia*, Tome III, pp. 251–288, 1927 is useful. For the Far East we have Lundblad, p. 370 (see reference above), which gives a list of genera and species. There is still much to be desired in the literature of the Gerridae.

VELIIDAE: W. E. China and R. L. Usinger have given us a key to the families of the Gerroidea and a key to the subfamilies and genera of Veliidie in *Annals and Magazine of Natural History*, Ser. 12, Vol. ii, pp. 343–354, 1949. This is a most welcome contribution. Of the twenty-one genera of Veliidae that they key out, only three are widely known. These are *Velia*, *Microvelia*, and *Rhagovelia*. *Velia* is now being studied by Dr. L. Tamanini of Italy. *Microvelia* contains many species in various parts of the world. Except for regional keys like that of Lundblad, p. 368 (reference above), no general key is available. For the Western Hemisphere we now have "Concerning the Genus *Microvelia* containing a check list of the American Forms", by Carl J. Drake and Roland F. Hussey, *The Florida Entomologist*, Vol. 38, No. 3, pp. 95–115, 1955. They list seventy species for which there are no adequate keys. For the Eastern Hemisphere I have some eighty-four species in my catalogue. Dr. Poisson has described thirty of them from Africa and Madagascar, and Dr. Hoberlandt adds seven more from Africa. Poisson keys out fourteen African species, and Hoberlandt gives a key for the Egyptian species. Dr. Lundblad, p. 369 (reference above) gives a key for some of the species in the Far East.

The genus Rhagovelia is in better shape. We have "Die Altweltlichen Arten der Veliidengattungen *Rhagovelia* und *Tetraripis*", by O. Lundblad, *Arkiv. För Zoologi.*, Bd. 28, A, No. 21, pp. 1–63, Taf. 1–13, 1936, and "The Genus *Rhagovelia* of the Western Hemisphere", by John Bacon, *University of Kansas Science Bulletin*, 1956.

My original interest was in the biology and ecology of the aquatic and semiaquatic Hemiptera, but the taxonomy of these insects was in such a sad state that taxonomy had to be studied first. In my time O. Lundblad of Sweden, T. Jaczewski of Poland, Raymond Poisson of France, W. E. China of England, Teiso Esaki of Japan, G. Evelyn Hutchinson in Africa and India, J. A. DeCarlo of Argentina, R. L. Usinger and his students in California, C. J. Drake and H. M. Harris in Iowa, H. M. Hale in Australia, R. F. Hussey in Florida, and recently Ludvik Hoberlandt in Czechoslovakia and L. Tamanini in Italy have made splendid contributions. A lot of work has also been done at the University of Kansas, and I hope to live to see papers available for the identification of species in all the genera, but before that can be done we will have to reach some stability in our concept of genera in some of the families.

The Periodical Cicada Complex (Homoptera: Cicadidae)

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ABSTRACT

In the more than one hundred years since Dr. J. C. Fisher described Magicicada (=Cicada) cassinii *from individuals taken with specimens of Brood X of* M. (=Cicada) septendecim, *officially the periodical cicada, many conflicting views have been put forth concerning the validity of the specific status of the smaller form.*

A map showing the localities from which we have records of Brood XIII, photographs showing color pattern and size variation in both sexes, drawings of structural differences of males found to be consistent, and analyses of the songs of both species are presented.

In general we found these two species to be sympatric, synchronic, and synhymnal, and to exhibit no tendency toward division of range other than local congregation apparently as a result of song attraction. This latter indicates that sound production and response may function as a behavioral isolating mechanism between the two species. Males of each species produce three distinctly different sounds which we have referred to as 1) the congregational song, 2) the courtship song, and 3) the protest squawk.

The recognition of M. cassinii *as a species distinct from* septendecim *again opens the question of the status of the entities previously considered to be thirteen-year forms of the periodical cicada.*

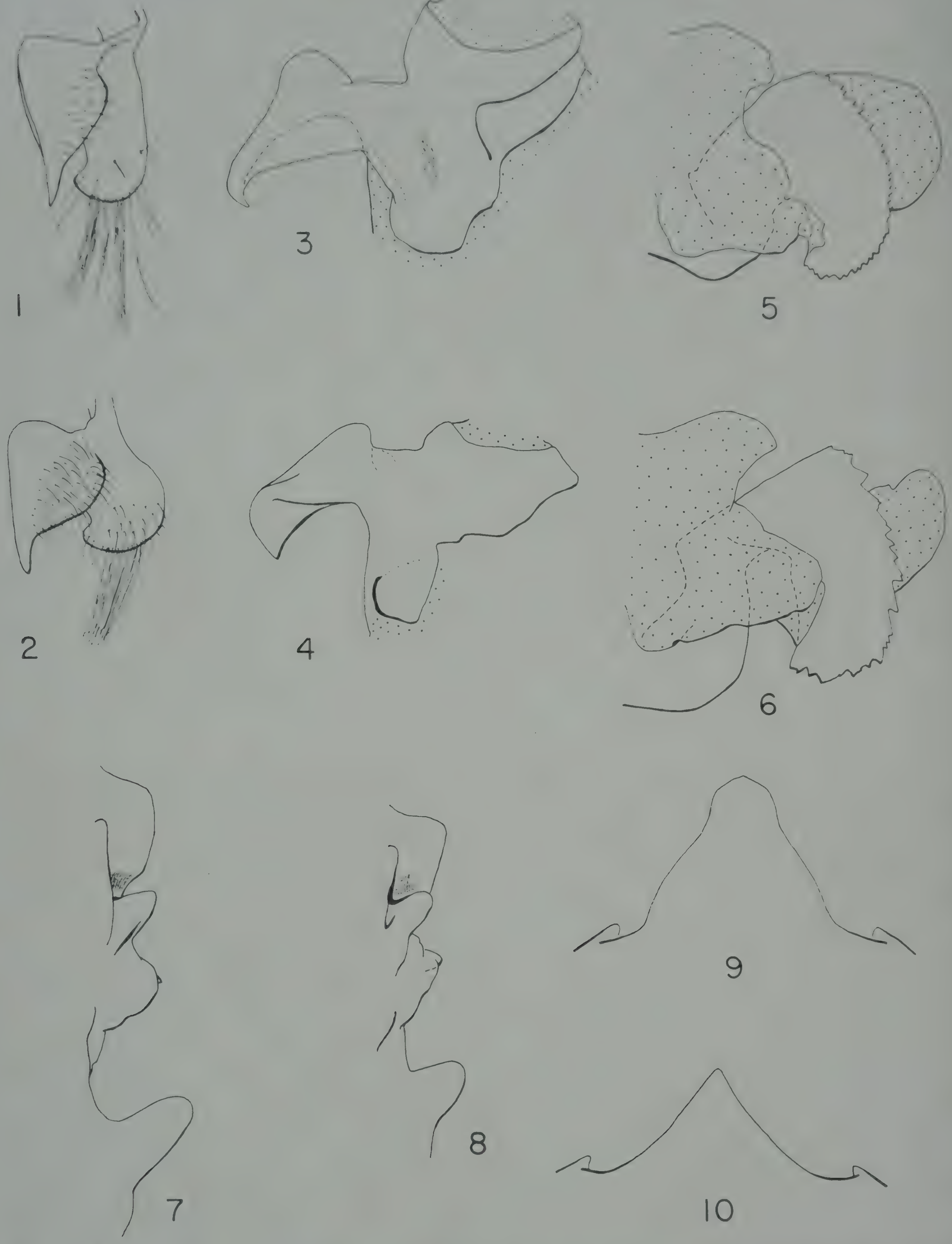
The work which we are reporting here was begun by the senior author as a project of the Illinois Natural History Survey, Urbana, and had its beginning in a cursory survey of the dispersal of Brood X in Illinois in 1953. At that time we became aware of certain song, color, and structural differences between recognizable forms in one or two places in Illinois. The emergence of Brood XIII in the spring of 1956 gave us an opportunity to check the occurrence of these forms in an emergence primarily centered in Illinois, allowing easy coverage of almost the whole range.

Magicicada cassinii was described by Fisher in 1851 (Brood X) and for a time was considered distinct from *septendecim* Linnaeus, 1758. Various opinions have been expounded as to the status of this entity since then, with the consensus in the last twenty years or so being that only one species, *septendecim*, but three forms were involved. We now believe that at least two very distinct species are involved in this complex, both of which have a seventeen-year life cycle. There likely are others occurring as thirteen-year forms.

Figs. 1–10 show various male structures which have proven to be consistently different between the two species. The apical aedeagal plates bearing toothed margins (Figs. 5 & 6) are best distinguished on the basis of shape, especially the angle between the top margin and the toothed edge. The teeth on the plates of *cassinii* are not always relatively more coarse than in *septendecim*. There is obviously a similarity in structure of these parts, just as one would expect to find between closely related species. The structures illustrated compare very favorably with those of specimens from Brood X taken in Illinois in 1953 and in Michigan in 1936.

Ventral abdominal color patterns are shown in Figs. 11–25. In males of *M. septendecim* (Figs. 11–14) the red-orange markings, indicated by the lighter areas, tend to spread basally at the margins of the sternites and these males always have rather broad orange markings. *M. cassinii* males which bear red-orange markings (Figs. 15–17) generally have these restricted to the apical margins of the sternites and not spreading basally at the sides. Many *cassinii* males have the abdominal sternites completely melanistic as in Fig. 18.

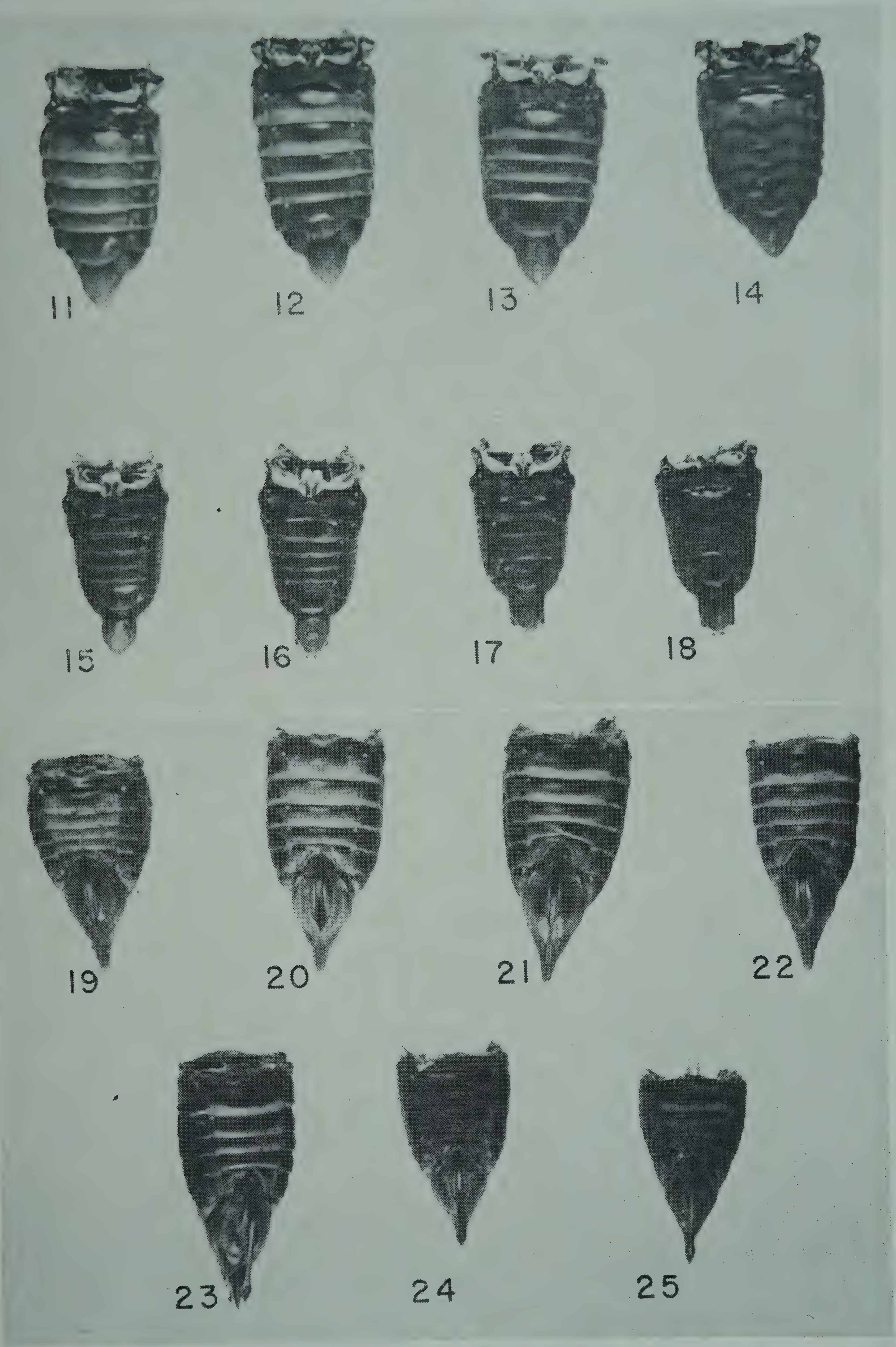
A general trend in ventral abdominal coloration similar to that shown above for males holds true for females of *septendecim* (Figs. 19–23). Although many specimens lack the



Figs. 1–10. Odd numbers are of *M. septendecim*, even numbers of *M. cassinii*: 1 and 2, caudal aspects of the dorsal hooks of the tenth abdominal segment; 3 and 4, lateral aspects of the same; 5 and 6, lateral aspects of the apex of the aedeagus; 7 and 8, oblique lateral aspects of the lateral margin of the ninth abdominal segment; 9 and 10, dorsal aspects of the dorsal prolongations of the ninth abdominal segment.

marginal spread, all have relatively broad apical bands of red-orange on the sternites. Females of *cassinii*, however, seldom have orange markings on the abdominal sternites, and when present they usually occur only as narrow apical bands on a few basal sternites (Figs. 24–25).

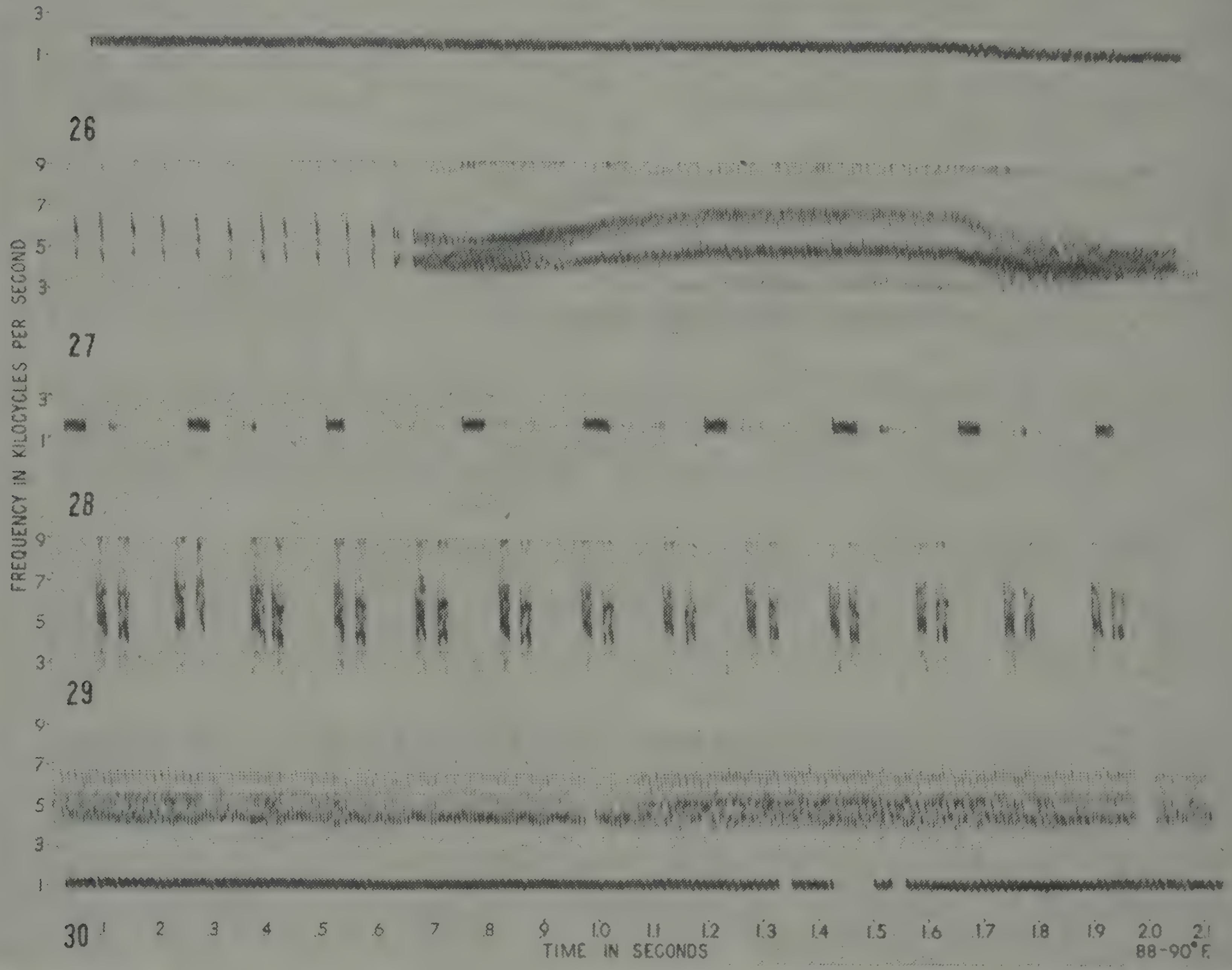
In general individuals of *M. septendecim* are larger than those of *cassinii*, but the size ranges for both sexes overlap for both species. By measuring the distance from tip of postclypeus to apex of ninth abdominal segment for males or to tip of ovipositor sheath



Figs. 11–25. Ventral aspects of abdomens: 11–14, *M. septendecim* males; 15–18, *M. cassinii* males; 19–23, *M. septendecim* females, 24–25, *M. cassinii* females.

for females and rounding off to the nearest half millimeter, we found the following average size classes for the two species: *M. cassinii:* ♂—24 mm., ♀—25mm.; *M. septendecim:* ♂—30mm., ♀—30mm.

Periodical cicadas produce sounds in the three general types of situations described by Alexander (1957). Audiospectrographs of the three different sounds made by both *septendecim* and *cassinii* are shown in Figs. 26–30. The songs from which these analyses were made were recorded under natural conditions in a wooded area near Hinsdale, DuPage County, Illinois, during June, 1956. The recordings were made at a tape speed of fifteen inches per second, with a Magnemite tape recorder, Model 610EV (Amplifier Corporation of America), using an American Microphone Company D33A microphone. The audiospectrographs were made with a Vibralyzer, the use of which is explained by Borror and Reese (1953). A total of 50 minutes of recordings were made, including 201 congregational songs of 49 males of *M. septendecim* and 150 congregational songs of 35 males of *M. cassinii*. Two hundred forty-six courtship phrases of two males of *M. septendecim*, and 1228 courtship phrases of seven males of *M. cassinii* were recorded. The temperature varied from 87° F. to 97° F. during recording.



Figs. 26–30. Audiospectrographs of the songs of *M. septendecim* and *M. cassinii*. (Relative intensities are shown by darkness of the mark): 26, A single phrase of the congregational song ("Pharaoh" call) of *M. septendecim;* 27, a single phrase of the congregational song of *M. cassinii;* 28, several phrases of the courtship song of *M septendecim*. (The faint marks between phrases are the songs of other individuals in the background); 29, several phrases of the courtship song of *Magicicada cassinii;* 30, protest squawking of *M. septendecim* (lower) and *M. cassinii* (upper).

Periodical cicada males do not space themselves apart in the field and perch and sing in the same spot day after day as do the males of most singing Orthoptera. Rather, a male delivers a few calls, flies a short distance — sometimes a few inches, sometimes several yards — and sings again. A bushful or treeful of singing cicadas thus seems to be in constant motion, if watched carefully. Although the males fly much more readily than do the females, the latter fly when disturbed, and fully as well as do the males. Presumably the congregational songs function in drawing the males and females of each species together. Individual females are probably only rarely attracted to individual males by the congregational song because of the constant moving about by the males while singing, and the congregation of large numbers of males into close proximity.

Figs. 26 and 27 are audiospectrographs of single calls from the congregational songs of *septendecim* and *cassinii*, respectively. In both species these are produced in series of one to five calls which are separated by short bursts of wing motion generally resulting in flight. Within series the individual calls last two to four seconds and are produced at intervals of 0.5 to two seconds. The rhythm of the two calls is radically different, as is generally the case with the songs of closely related sympatric species of Orthoptera and Cicadidae.

The rate of pulsation due to the individual vibrations of the tymbals in the call of *septendecim* varies from 120 to 160 per second, while the call of *cassinii* involves two different pulse rates. The first part of the call sounds like a series of rapid ticks, while the second part sounds buzzy to the ear, more like the call of *septendecim*. The ticks are produced at a rather irregular rate of 16 to 25 per second, while the individual pulses in the buzz are produced at a rate of 180 to 210 per second. *M. cassinii* frequently begins the ticking part of its congregational call while walking or flying about, though, like *septendecim*, it does not move about during the buzzing part of the song. Occasionally an individual produces the ticking part of the call and does not follow with the buzz, or produces ticks both before and after a buzz. The two-part character of the congregational song of *cassinii* provides an additional rhythmic or uniform interval in the song of this species, as compared to that of *septendecim*.

The call of *septendecim* has a rather narrow band of intense frequencies located between one and two kilocycles per second. The call of *cassinii* is somewhat higher-pitched, and has a wider band of intense frequencies located between four and seven kilocycles per second. If the sound-producing structures are similar, a smaller insect produces a higher-pitched sound than a larger specimen, either in the same species, or in a different one. The rise and drop in pitch in the calls of these two species corresponds to a raising and lowering of the abdomen. The mechanics of this abdominal movement and associated changes in tymbal tension have been treated by Pringle (1955) for other cicada species.

A recording of a chorus of periodical cicadas made by D. J. Borror and R. W. Champlain in June, 1953, in Delaware County, Ohio, contains both of the congregational songs described here for *M. septendecim* and *M. cassinii* from Brood XIII in Illinois. Although the number of individuals singing in this recording makes it impossible to analyze the songs in detail, they seem identical to those described here.

Males of both *septendecim* and *cassinii* produce distinctive sounds under certain conditions when in close proximity to females. These will be referred to as courtship songs and are portrayed in Figs. 28 and 29 for *septendecim* and *cassinii*, respectively. The rates of delivery of the individual phrases of the courtship song varied from 3.6 to 4.8 per second in *septendecim*, and from 3.6 to 6.7 per second in *cassinii*. During courtship, and while producing this sound more or less continuously, the male crawls over the female, moving his partially extruded genitalia about on the ventral surface of her abdomen until the genitalia are engaged or he is dislodged.

The few instances of interspecific courtship observed in cages during this study were unsuccessful. An examination of more than 150 mating pairs, including approximately equal numbers of both species, yielded no cross-matings. The proportion of copulating pairs encountered in the field is highest in late afternoon.

Male cicadas almost invariably vibrate their tymbals when handled, or when captured by birds or provisioning wasps. Fig. 30 portrays the protest squawks of both *septendecim* (lower) and *cassinii* (upper) on the same audiospectrograph. The difference in frequency and pulse rate are evident. These sounds are so different that a male of either species can be identified easily by the sound he makes when captured.

The congregational song of *M. septendecim*, the so-called "Pharaoh" call, is produced from dawn until late afternoon, and thousands of individuals singing together produce an uninterrupted din in which the individual calls are completely indistinguishable. *M. cassinii*, on the other hand, sings chiefly in the afternoon, and local groups of males sing together in bursts which are separated by intervals in which none or only a few males are singing. When an individual breaks such a silent period by beginning a song, he is invariably joined by a number of males in the vicinity, and the chain reaction continues until the whole local population is involved. One by one the males finish their burst of song and drop out, and the whole cycle is repeated over and over again.

Several of the recordings made of choruses of males of *M. cassinii* singing together indicate that an imperfect synchronization of the ticking and buzzing parts of the song is accomplished by groups of individuals in close proximity. At any single time practically all of the males involved in song are either ticking or buzzing together. This imperfect synchronization, in which the beginning of song by one male is apparently the stimulus, also occurs in the meadow grasshoppers (Conocephalinae), which likewise produce songs that involve two distinctly different pulse rates and thus closely resemble the congregational song of *M. cassinii*. Synchronization of individual calls and of song bursts by *cassinii* both indicate that *cassinii* males are stimulated by their own song rather than by those of the *septendecim* males which are usually singing continually all around and among the *cassinii* individuals.

Both *M. septendecim* and *cassinii* are very sensitive to daytime changes in light intensity, and will usually stop singing if a cloud obscures the sun. On one occasion both species stopped singing after a sudden drop in light intensity during which a rather brisk rain shower began. During the shower the sun reappeared, and although the rain did not slacken, both species instantly burst into song. The light sensitivity of both species apparently changes during their daily singing period, for both begin singing at intensities quite different from those at the time that they cease singing. At night, short bursts of protest squawks by *cassinii* are continually heard near street lights and along roads with frequently passing cars. Males of *septendecim* in the same areas remain silent, even though they may be much more abundant. This may reflect a lower threshold of irritability in *cassinii* which is also indicated by the fact that individuals are disturbed into flight more easily than those of *septendecim*. These factors probably explain, at least in part, why very few specimens of *cassinii* are captured by the average collector.

We believe that the consistent and radical differences between the songs and singing behavior of these two otherwise quite closely related species is a strong indication that song is important in at least reinforcing their reproductive isolation. Such differences seem to appear quickly between sympatric species of singing Orthoptera and Cicadidae, often preceding noticeable differences in morphology or other characteristics (Alexander, unpublished data).

The map in Fig. 31 shows the area in which Brood XIII was expected to occur, based on Marlatt (1923), as indicated by the shaded lines. The black dots indicate the location of records taken in 1956. These records are of many types. Most of them are based on specimens collected by the authors, or are auditory records (i.e., represent localities where songs were heard by the authors). Some are based on reliable auditory or damage records made by others; some are based on specimens submitted by others; some are based on published records of occurrence appearing in the *Cooperative Economic Insect Report.* In practically every locality for which we have data the two species occurred together, differing in mumerical proportions sometimes from shrub to shrub, from tree to tree, or from city block to city block, but always occurring together. Our data do not indicate specific differential selection with respect to host plants, slope of terrain, soil type, drainage, or any other ecological factor.

The following is a summary of our 1956 localities and dates of collections: ILLINOIS: Brookfield, Chicago Heights, Downers Grove, N Dwight; S Elburn, N Greenview, Henry, Hinsdale, Joliet, Kappa, LaGrange, Libertyville, Lowell Park (Dixon), Mackinaw R. along U. S. 150 (Woodward Co.), Magnolia, Marseilles, Mokena, Moline, Morris, Oregon, Ottawa, Palos Park, Paris, Park Forest, Peoria, Pontiac, River Grove, Sandwich, N E Springfield, Urbana, Western Springs; April 1—June 17 (nymphs of septendecim), May 28—July 6 (adults). INDIANA: Crown Point, Lake Co., La Porte Co., Porter Co.; July 11—16 (adults). IOWA: N W Bell Plaine, Johnson Co., Lin Co., Tama Co., N E Tama; June 12—23 (adults), July 8 (damage). OHIO: Hocking Co.; June (adults). VIRGINIA: Montgomery Co.; May 30 (adults). WISCONSIN: Beloit, Grant Co., Iowa Co., Lafayette Co., Richland Co., Rock Co., Walworth Co.; June 9 (adults and nymphs).

In addition to the above, periodical cicadas were tentatively reported from an orchard in Houston County, Minnesota. Unfortunately no specimens were taken and the record cannot be verified. This is of particular importance because no verifiable record is available for that state, and because *Okanagana canadensis* occurs at the same time of the year in

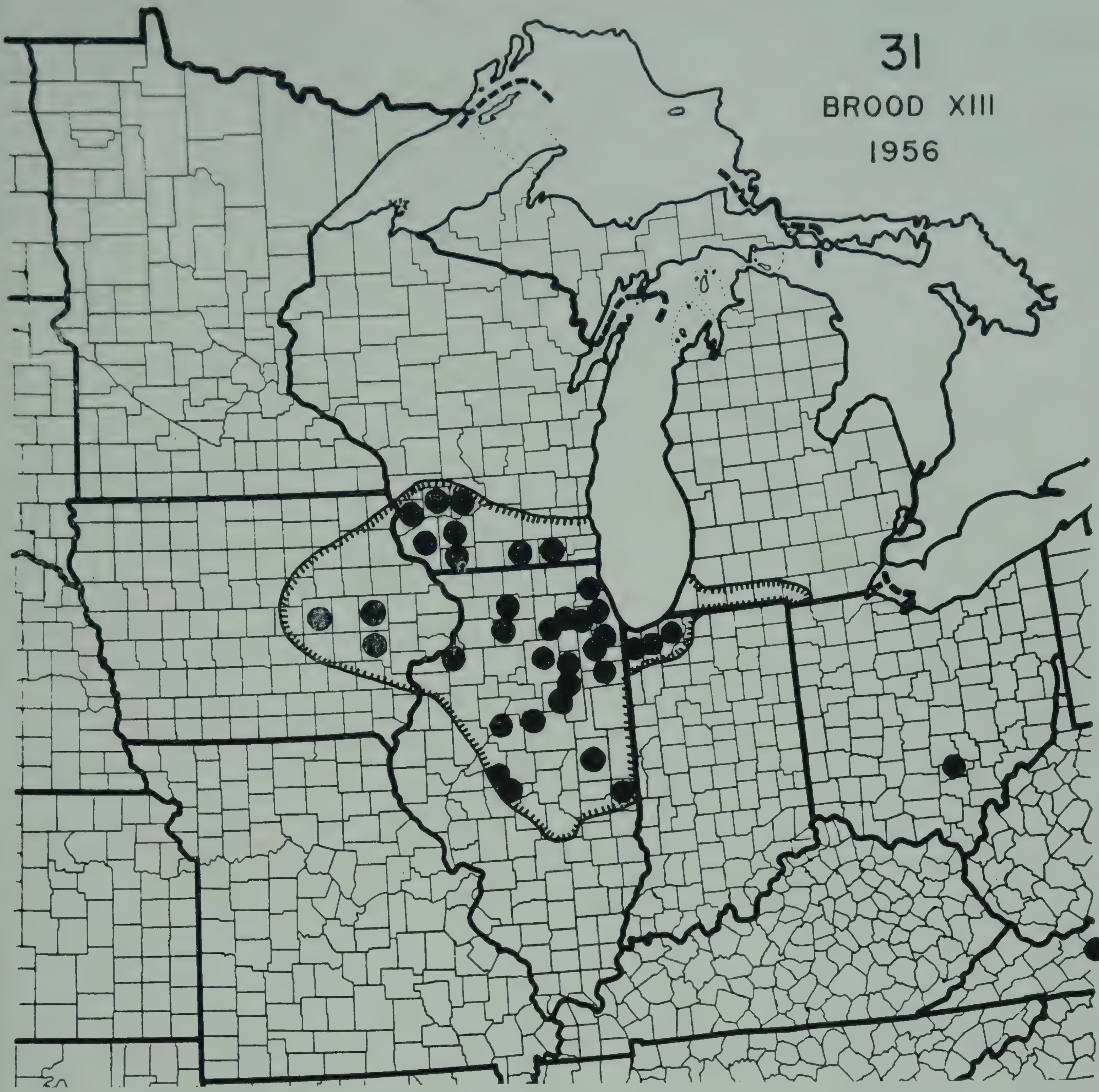


Fig. 31. Map of the expected range and location of records for both species in Brood XIII, explanation in text

that area, and closely resembles periodical cicadas in coloration, in type and appearance of damage, and in size and suddenness of emergence.

In conclusion, the recognition of two seventeen-year species suggests the possibility of other species among the thirteen-year forms of what formerly was considered to be one species. Both large and small thirteen-year forms have been reported, too. It seems unlikely that both seventeen-year species have evolved thirteen-year forms maintaining similar relationships to each other. It seems more logical to expect to find additional species associated in this complex. So far we have not been able to examine sufficient authentic thirteen-year material to establish or refute the validity of this expectation. We hope to gain more information by following up Brood XIX, the largest thirteen-year brood, in 1959 in the same manner that we studied Brood XIII.

REFERENCES[1]

Alexander, R. D. 1957. Sound production and associated behavior in insects. *Ohio Jour. Sci.* 57: 101–113, 1 Text Fig., 4 Plates.

Anon. 1956. *Cooperative Economic Insect Report* 6 (25): 580, 593; (26): 612; (27): 646.

Borror, D. J., and C. R. Reese. 1953. The analysis of bird songs by means of a vibralyzer. *Wilson Bull.* 65 (4): 271–276, 7 Figs.

Fisher, J. C. 1851. On a new species of cicada. *Proc. Acad. Nat. Sci. Philadelphia* 5: 272–273.

Linnaeus, Carolus. 1758. Systema Naturae. Regnum Animale. Tenth Edition. Holmiae. 824 + iii pp.

Marlatt, C. L. 1923. The periodical cicada. *U. S. Dept. Agric. Bureau of Ent., Bul. No.* 71: 183 pp.

Pringle, J. W. S. 1954. A physiological analysis of cicada song. *Jour. Exp. Biol.* 31: 525–560, Text Fig. 2, Plate 11.

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[1] Since submission of this manuscript the authors have published an experimental investigation of the functions of *Magicicada* songs (*Ohio Jour. Sci.* 58: 107–127, 16 Figs. March, 1958).

The Taxonomic Value of the Male Genitalia in Leafhoppers in the Light of New Studies on the Seasonal Forms of *Euscelis*

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ABSTRACT

As a warning example against unrestricted use of male genitalia in taxonomic work, the relations of the European species of the leafhopper Euscelis *are demonstrated. The specific polymorphism of the flattened penis point only permits a confined clearing of the synonyms in the striking likeness of species. Systematic catches all over the year and extensive breeding experiments through many generations prove that altogether six, but probably eight or ten, out of fourteen species hitherto distinguished by means of penis morphology belong together to only two seasonal form-cycles* (Euscelis plebejus *and* Euscelis lineolatus). *In these, spring- and summer-forms show much greater differences in the formation of the penis point than nearly related but genetical separated species. Form and size of the penis point are mainly induced by the photo-period during larval development. According to the findings in the open air the spring form results from short days up to sixteen hours daylight, the summer-form only from long days with more than sixteen hours light regime. Other environmental factors only modify the penis form already induced photoperiodically.*

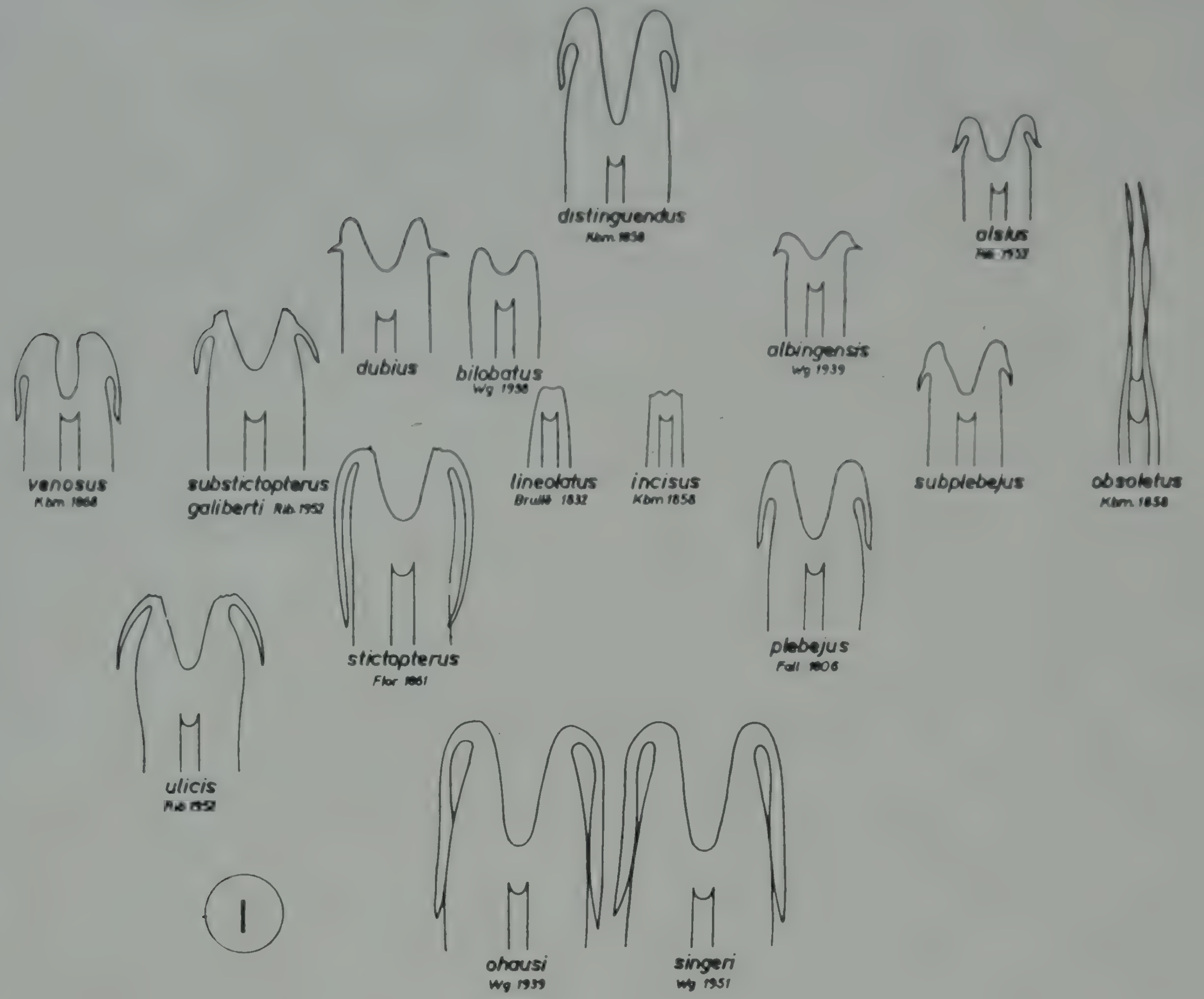
In many insect orders it is often difficult or impossible to find external signs in differentiating closely related species. Frequently also the extensive overlapping of their variation spread prohibits the taxonomic application. In such cases as in Coleoptera, Lepidoptera, Diptera, and others, the morphology of male genitalia, which often are manyfoldly formed, is used with great success, although a troublesome preparation is mostly unavoidable. Many systematic and phylogenetic investigators from this apparently specific constancy of male genitalia have concluded penis and vagina to fit as key and lock, producing a barrier against copulations of nearly related species. Recently evidence is increasing that often this does not come true; and in many cases the male genitalia also vary in a manner, which forbid their taxonomic use.

A special surprising example offers the situation in the leafhopper genus *Euscelis* (Brullé). In the recent restricted conception of Ribaut (1952), it would comprise twenty-one species, described before 1900, that is by the aid of the extremely variable colour and fine spotted pattern only. How difficult it was to differentiate these twenty-one species proves the fact that by the aid of penis morphology by Wagner (1939) and Ribaut (1952) their number could be diminished to seven, clearing many synonyms. New descriptions of these authors, however, increased it again to about fourteen. Apparently the penis form also was a bad taxonomic groundwork.

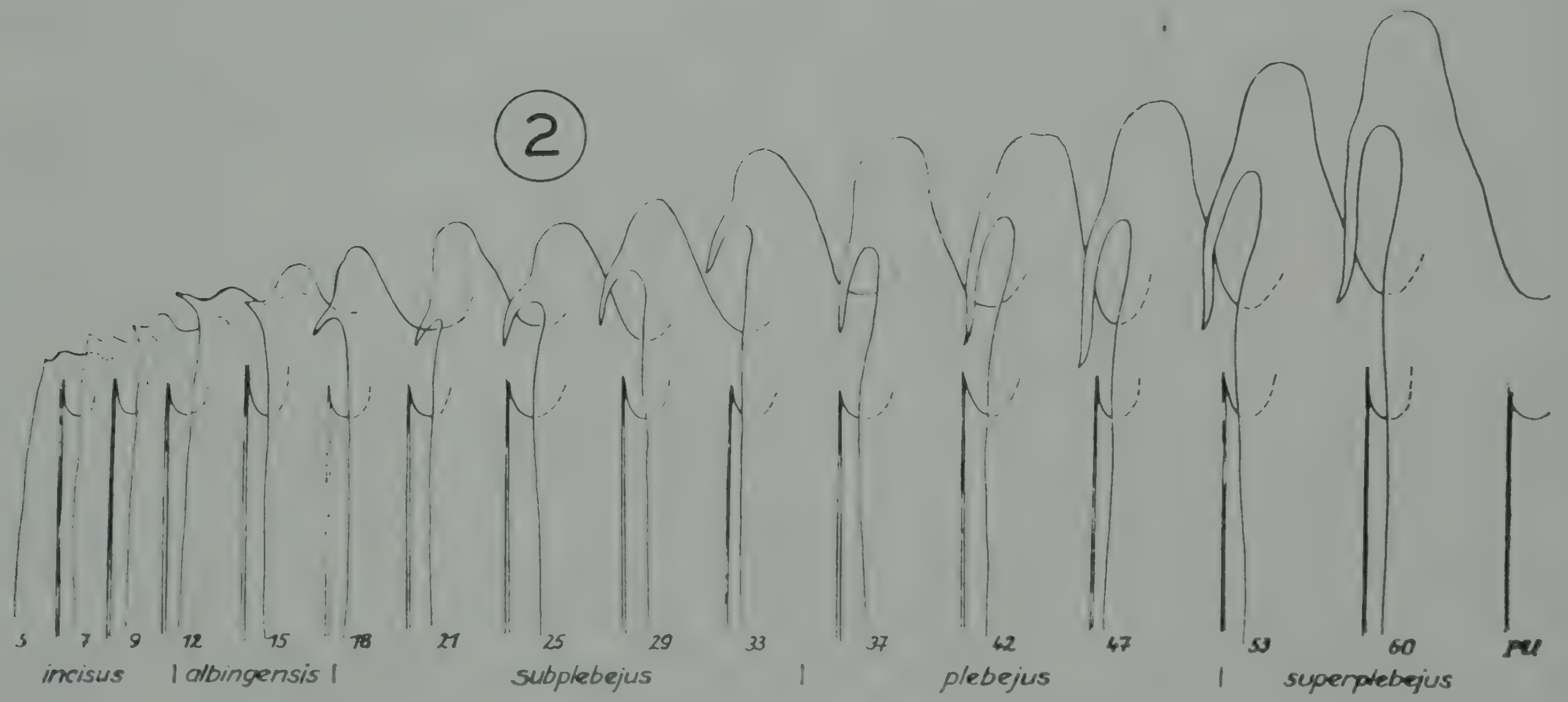
The penis of *Euscelis* (sensu stricto) is marked out by a more or less broad, ribbon-like, flattened point, which can be modified in a manyfold manner by an apical sinus and differently formed lateral spines. Looking over the penis forms already described (Fig. 1) one would suppose them belonging to clear cut species without any doubt. Scruples arose first as Wagner, by comparing much material, found a continuous row of penis forms from *Euscelis incisus* Kbm. to *albingensis* Wg. and *plebejus* Fall. (Fig. 2). But because the different links of this row appear in very different frequencies and only during distinct seasons, I suspected a case of seasonal dimorphism.

Studying a great collection, collecting regularly in distinct habitats all over the year, and especially repeating breeding experiments through two and more generations, I proved that *Euscelis incisus* is in fact the spring from and *Euscelis plebejus* is the summer form of one species, the name of which is now from priority *Euscelis plebejus* Fall. In the open air, therefore, one generation of the *incisus* form always alternates with one generation of the *plebejus* form, because the species is facultative bivoltine.

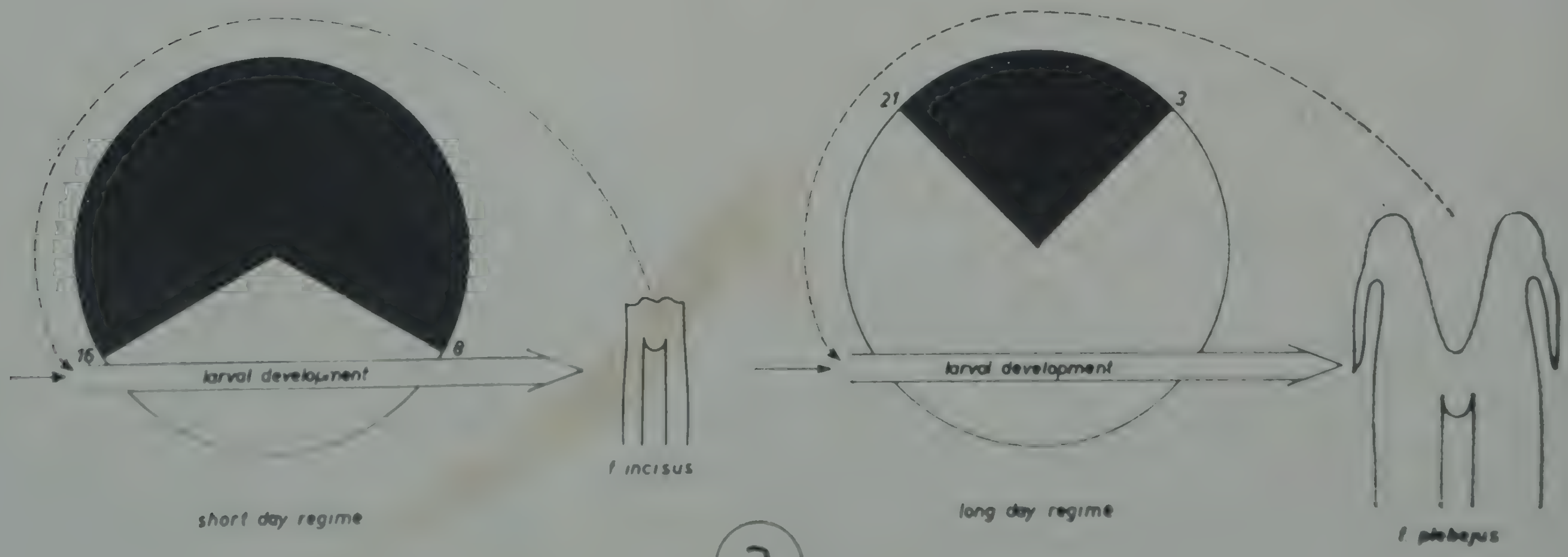
The formation of the rarely collected intermediate forms becomes comprehensible only by the investigation of the factors stamping the seasonal modifications. For these especially the photoperiod is decisive, ruling during the larval development (Fig. 3). *Incisus* forms are developed if the daily light regime lasts between four and fifteen hours, *plebejus*


distinguendus
Kbm. 1858
alsius
Rib. 1953
dubius
bilobatus
Wg 1938
albingensis
Wg 1939
venosus
Kbm 1868
substictopterus
galiberti Rib. 1952
lineolatus
Brullé 1832
incisus
Kbm 1858
subplebejus
obsoletus
Kbm. 1858
stictopterus
Flor 1861
plebejus
Fall. 1806
ulicis
Rib. 1952
ohausi
Wg 1939
singeri
Wg 1951

①


PU
incisus
albingensis
subplebejus
plebejus
superplebejus

②


16
8
larval development
♀ incisus
short day regime
21
3
larval development
long day regime
♀ plebejus

③

forms on the contrary arise in light periods of more than sixteen hours. This agrees with the conditions in the open air. The *incisus* larvae develop in autumn, and, after a dormancy period in spring during short days, the *plebejus* appear in June and July during long days. In breeding experiments, there are produced *incisus* generations to any amount by short days and corresponding as many *plebejus* generations without interruption by long day conditions (Fig. 3). Intermediate forms as *albingensis* and *subplebejus* are formed if in hot and dry years the development is so accelerated that the larvae of an additional third generation grow up in summer at first in long days, later on in short days. In experiments they also are formed, if for instance the three first stages run in short day periods and the two final ones in long day.

Temperature, humidity, and quantity or quality of nutrition can neither replace the effect of the photoperiod nor correct the seasonal form induced by it, but can only modify gradually. Higher temperatures, dry air, or abundance of fit nutrition increase the penis dimensions, while low temperatures, humid air, or scarcity of food decrease them. As a scale we use the size of the outline of the penis in the height of the ductus ejaculatorius.

How exactly the penis form reacts to the differences in environmental factors, shows a statistical analysis of 341 males of *Euscelis plebejus*, collected in August, 1955, about one-third in fields of alfalfa and meadows and about two-thirds in orchards. In the cool and humid shade of old cherry trees, the day length in the late summer sinks below the critical length of sixteen hours sooner than in the open fields. Therefore the outlines of the penis points of the males in the orchards are smaller than those of the open fields (Fig. 4), where the required brightness lasts longer, and also higher temperature and lesser humidity advance the growth of the penis.

It was obvious to seek for resembling relations in other species of *Euscelis*. In fact extended breeding experiments establish that also the Mediterranean and west European species *Euscelis lineolatus* Brullé, *bilobatus* Wg., and *stictopterus* Flor inclusively *Euscelis galiberti* Rib. and a few undescribed forms belong to only one form cycle, which now retains the oldest name of *lineolatus* (Fig. 5). In this the smaller *lineolatus* and *superlineolatus* forms arise at day light of less than sixteen hours, the larger *bilobatus*, *dubius*, and *stictopterus* forms under light regimes of more than sixteen hours daily. Curiously the spineless forms are found in the whole territory of the species to England in the north, but the spined ones, specially *stictopterus*, on the contrary occur only in the Mediterranean region and in southern France, and very seldom in the Netherlands. Breeding experiments proved that pure *stictopterus* generations only develop in daylight of more than eighteen hours and at day temperatures of more than 27°C. Therefore the *stictopterus* form represents a warm-modification of the long day form while *bilobatus* is the form of the cooler climate.

In consequence of the reported results, the number of European species of *Euscelis* diminishes considerably (Fig. 6). The centre is formed by the two great form cycles of *Euscelis lineolatus* and *Euscelis plebejus*, with the former species now degraded to seasonal modifications: namely, *incisus*, *albingensis*, *bilobatus* and *stictopterus*, to which probably are to add the species described by Ribaut 1952: *alsius* as a form of *subplebejus*, and *galiberti* and *ulicis* as forms of *substictopterus*. Only the univoltine species *Euscelis distinguendus* Kbm., *venosus* Kbm., *obsoletus* Kbm. and *ohausi* Wg. continue as independent species. In view of the variability of penis forms in *Euscelis*, the author of *Euscelis singeri*, W. Wagner, feels inclined now to consider this species identical with *ohausi*. *Euscelis obsoletus* stands aside both in penis morphology and other attributes. The great resemblance between the penes of *Euscelis plebejus* and *Euscelis distinguendus* urged Wagner (1939) to put them in the same cycle. But not any one of our 8000 bred or collected males of *plebejus* shows a *distinguendus* type.

These univoltine species are armed with penis forms of long day habitus like *plebejus* and *stictopterus*. Their larvae develop in fact at the long days of midsummer. One could imagine them to form also a short day penis like *incisus* or *lineolatus*, if they were subjected to conditions of a short daily light regime. But breeding larvae of *Euscelis ohausi* at eight

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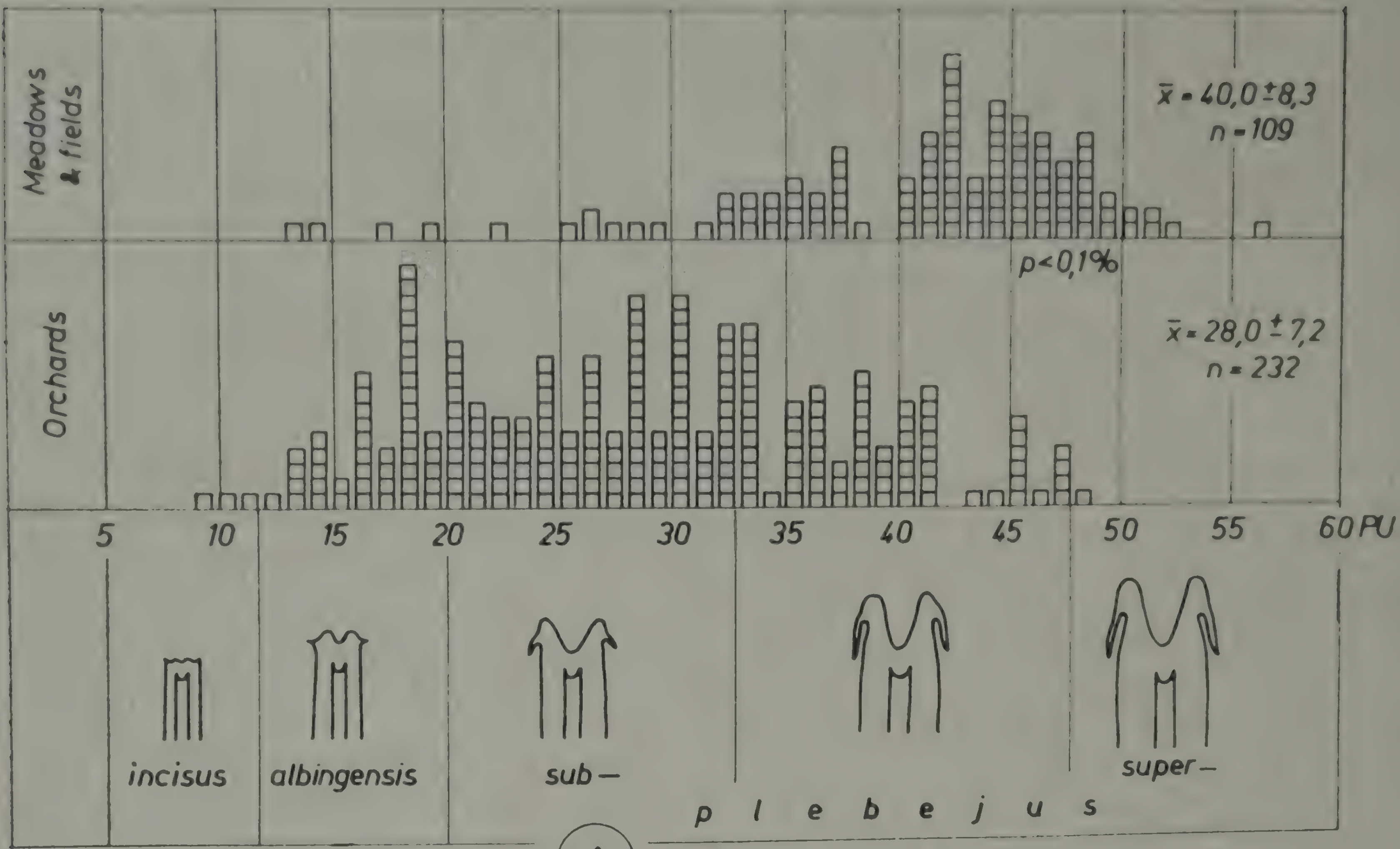
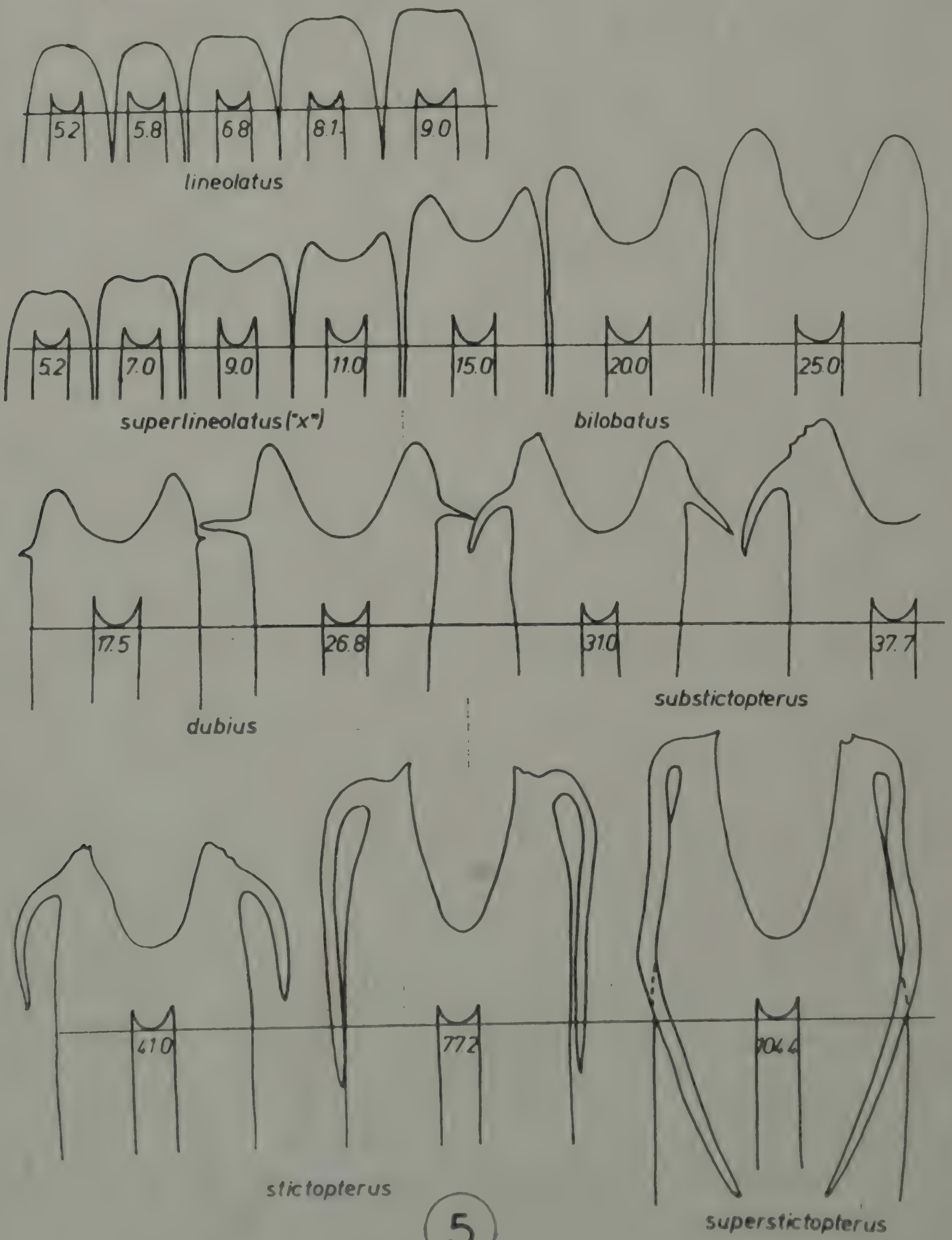
← Fig. 1. The European species hitherto described of the leafhopper genus *Euscelis* Brullé (sensu Ribaut 1952) represented by their taxonomically used penis forms. Fig. 2. The eunomic row of the penis forms from *Euscelis incisus* to *Euscelis albingensis* and *Euscelis plebejus* as arranged by W. Wagner. Fig. 3. The influence of the photoperiod on the penis form of *Euscelis plebejus*, causing its seasonal forms in the natural course of the year.


Meadows & fields
x̄ = 40,0 ± 8,3
n = 109
p<0,1%
Orchards
x̄ = 28,0 ± 7,2
n = 232
5
10
15
20
25
30
35
40
45
50
55
60 PU
incisus
albingensis
sub—
super—
p l e b e j u s

④


5.2
5.8
6.8
8.1
9.0
lineolatus
5.2
7.0
9.0
11.0
15.0
20.0
25.0
superlineolatus ("x")
bilobatus
17.5
26.8
31.0
37.7
dubius
substictopterus
41.0
77.2
104.4
stictopterus
superstictopterus

⑤

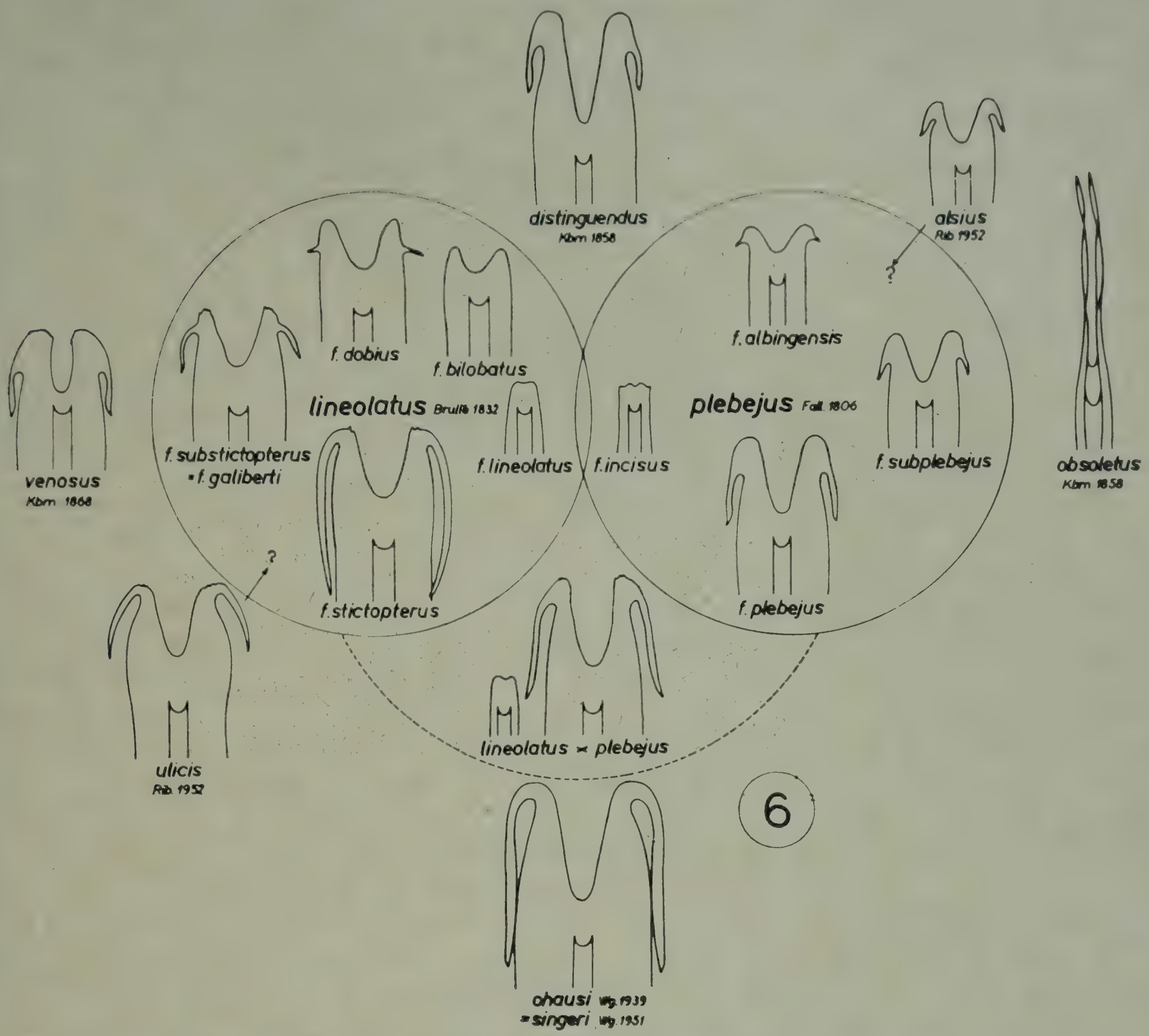

distinguendus
Kbm 1858
alsius
Rib 1952
?
f. dobius
f. bilobatus
f. albingensis
venosus
Kbm 1868
lineolatus Brullé 1832
plebejus Fall. 1806
f. substictopterus
= f. galiberti
f. lineolatus
f. incisus
f. subplebejus
obsoletus
Kbm 1858
?
f. stictopterus
f. plebejus
ulicis
Rib. 1952
lineolatus × plebejus
6
ohausi Wg. 1939
= singeri Wg. 1951

Fig. 6. The same penis forms of *Euscelis* as in Fig. 1 but after an analytical investigation of their genetic relationships. In the circles the seasonal form-cycles of *Euscelis plebejus* and *Euscelis lineolatus*, within the strokes their crosses and outside the uniform univoltine species.

hours of light per day, the adults possess the same penis form as at eighteen hours, although with a significantly reduced size. That means the penis form of the univoltine species is more strongly determined than in polyvoltine ones.

As the example of *Euscelis* demonstrates the environmental factors may be able to transform the shape of male genitalia of one species in so extreme a manner that modifications develop, which resemble one another lesser than those of nearly related species. These extreme seasonal forms of one Euscelis species are of course unlimitedly fertile mutually as experiments demonstrate. In our case therefore the key-lock-mechanism is not conclusive. But in breeding conditions the females of *Euscelis lineolatus* f. *lineolatus* also conjugate with males of *E. plebejus* f. *incisus* and produce intermediate crosses (Fig. 6). But these are not found in the open air, although both form cycles live together in western Europe; probably the copulation hindrance by different courtship behaviour being greater than by penis morphology.

The heuristic value of genital morphology for taxonomic purposes in many insect orders should not be contradicted by our examples, but they demonstrate the surprises to which an uncontrolled use may lead. Without any doubt there are similar cases in Auchenorrhynchas and perhaps also in other insect orders. For the taxonomist this may be bad news, but we may console ourselves with the fact that ecology is enriched by them in

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Fig. 4. The distribution of the frequency of penis forms (and sizes) of *Euscelis plebejus* specimens collected in open and shaded places during August, 1955, in northwestern Europe (1 PU = 0.015 mm. of the penis outline).
Fig. 5. The penis forms of the (seasonal) modifications of *Euscelis lineolatus* Brullé.

understanding an eco-morphologic connection hitherto unknown; for now we are sure that the classic cases of seasonal dimorphism of the Lepidoptera as in *Araschnia* are photoperiodically caused also.

REFERENCES

Müller, H. J. 1947. Saisondimorphismus bei Arten der Gattung *Euscelis*. *Bombus* 40: 173–174.

Müller, H. J. 1954. Der Saisondimorphismus bei Zikaden der Gattung *Euscelis* Brullé (Homoptera: Auchenorrhyncha). 3. Beitrag zur Biologie mitteleuropäischer Zikaden. *Beitr. z. Entomol.* 4: 1–56.

Müller, H. J. 1955. Die Bedeutung der Tageslänge für die Saisonformenbildung der Insekten, insbesondere bei den Zikaden. *Ber. 7. Wandervers. Disch. Entomol. Berlin* 1954: 102–120.

Müller, H. J. 1955. Die Saisonformenbildung von *Araschnia levana*, ein photoperiodisch gesteuerter Diapause-Effect. *Naturwiss.* 42: 134–135.

Müller, H. J. 1956. Über die Wirkung von Umweltfaktoren auf die Variabilität saisondimorpher Insekten, insbesondere der Gattung *Euscelis*. *Verh. Dtsch. Zool. Ges. Hamburg* 1956: 450–462.

Müller, H. J. 1957. Die Wirkung exogener Faktoren auf die zyklische Formenbildung der Insekten, insbesondere der Gattung *Euscelis* (Hom. Auchenorrhyncha). *Zool. Jb. Syst.* 85: 317–430.

Ribaut, H. 1952. Homoptères Auchénorhynques. II. Jassidae. *Faune de France* 57. Paris.

Wagner, W. 1939. Die Zikaden des Mainzer Beckens. *Jahrb. Nass. Ver. Naturkd.* 86: 77–212.

On the Use of the Thoracic Structure for the Classification of Females in the Genus *Pseudagrion* (Odonata)

By B. I. Balinsky
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Johannesburg, South Africa

ABSTRACT[1]

The use of genitalia in the classification of insects is based on the necessity for the copulatory organs of the male and female to correspond to each other. The peculiar type of copulation found in Odonata is carried out with the aid of special organs, such as the secondary genitalia on the second abdominal segment of the male. As the male grips the female on the junction of the pro- and mesothorax, these parts of the thorax have developed in some genera, notably among the Zygoptera, peculiar structures that facilitate a firm hold by the anal appendages of the male. In females of Pseudagrion, *special structures may be present on both the pro- and mesothorax. These structures differ from species to species and may be used for distinguishing females in the genus. There appears to be a correlation between the type of appendages of the male and the peculiar pattern of thoracic structure of the female, indicating that these parts have been dependent on each other in their evolution.*

[1] The full text of the paper has been published in the *Journal of the Entomological Society of Southern Africa* 20(2): 280-294. 1957.

The Systematics of *Tetragoneuria*, Based on Ecological, Life History, and Morphological Evidence (Odonata: Libellulidae)

By Edward J. Kormondy
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ABSTRACT[1]

The population-species concept is applied to the ecology, life history, and morphology of the genus Tetragoneuria. *Six taxa occurring in the Great Lakes region were studied during a four-year period.*

Adult males and females of Tetragoneuria cynosura, T. spinigera, *and* T. canis *are distinguished morphologically by secondary sex characters and by statistically significant differences in mensurable characters.*

Differences in geographic distribution and habitat, response to environmental stimuli, flight speed, seasonal occurrence, diurnal peaks of activity, and reproductive behavior are discussed. Similarities in length and northward progression of season, duration of life, explosive emergence, maturation period, and reproductive behavior are discussed. Physiological life histories (eclosion and growth rates, duration of stadia) are compared as are morphological developmental patterns. Morphological and statistical analyses are presented on the ultimate larval stage. Temperature influence promoting the extension of hindwing marking characteristic of two subspecies is shown as the presence of temperature-related clinal variation of a nonstepped nature.

The evidence from morphology, ecology, and life history: (1) affirms the validity of cynosura, spinigera, *and* canis *as distinct taxonomic entities of specific rank; (2) invalidates* T. morio, *synonymizing the male as* cynosura, *the female as* spinigera; *(3) recognizes the subspecies of* cynosura *and* spinigera *as clinal variants without taxonomic status.*

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[1] *Misc. Publ. Mus. Zool. Univ. Mich.*, No. 105 (In press).

An Inquiry into the Significance of the Larval Proventriculus in the Taxonomy of Odonata[1]

By Alice Ferguson–Beatty
Pennsylvania State University
University Park, Pa.

ABSTRACT

In attempting to determine the taxonomic usefulness of the larval proventriculus of Odonata, the writer reviewed the published work on this structure from its first appearance in 1852 to date, most of which was inconclusive so far as the diagnostic possibilities inherent in the proventriculus are concerned. The writer's present study involved comparative examination of the proventricular armature of thirty-seven genera and forty-three species of Odonata-Anisoptera from the Nearctic Region. The principal result of this study is a body of evidence showing that, in the families of Odonata-Anisoptera generally considered most primitive, the Gomphidae, Aeshnidae, and Cordulegasteridae, generically and even specifically diagnostic characters are often found in the armature of the larval proventriculus, while in the families considered more specialized, the Corduliidae and Libellulidae, the proventricular armature is so generalized that it has little value in taxonomy. However, it was found that sufficient differentiation of proventricular structure exists, between two groups formerly thought to be subfamilies of the Corduliidae, that separation of these groups on the family level is strongly suggested, in agreement with findings based on external structure. It was also found that there is sometimes greater discontinuity of proventricular structure between species contained in a single genus than between various genera that otherwise do not appear very closely related. Nineteen original figures illustrative of these findings are presented.

As early as 1852 the armature of the larval proventriculus of two species of Odonata was figured by Leon Dufour[2], and in succeeding years that of a number of species was figured incidentally in the work of several morphologists.[3] However, it remained for Friedrich Ris, in 1896, to employ this armature as a taxonomic character. In his published work the proventricular armature of unidentified species of *Gomphus*, *Cordulegaster*, *Aeshna*, and *Cordulia* was figured and discussed along with the armature (not figured) of *Epophthalmia* sp., *Diplax* sp. and *Libellula* sp., and on this basis these genera were categorized in substantially the same major groups as were already recognized on the familiar grounds of adult venation, head structure and genitalic characters. Ris also drew some broad phylogenetic conclusions which differ but little from those based upon external structure alone. Further significant work on the proventricular armature as a taxonomic character was that of Tillyard (1910, 1917), presenting figures of the armature of six species[4] and drawing further conclusions on relationships. Following Tillyard's discussion in his comprehensive treatise on the *Biology of Dragonflies* in 1917, several authors have presented figures and descriptions of the larval proventricular armature while describing new or unusual species[5], but no further comprehensive attempt has been made to utilize this structure in the definition of major or minor taxonomic categories.

The author's work to be discussed here involved comparative morphological study of the proventricular armature of forty-three species of Nearctic Odonata-Anisoptera, contained in thirty-seven genera. These entities were distributed through the major taxonomic categories indigenous to North America and were selected for the purpose of evaluating the armature of the proventriculus as a taxonomic character, both as diagnostic of major and minor categories and as an indicator of relationship and lines of descent.

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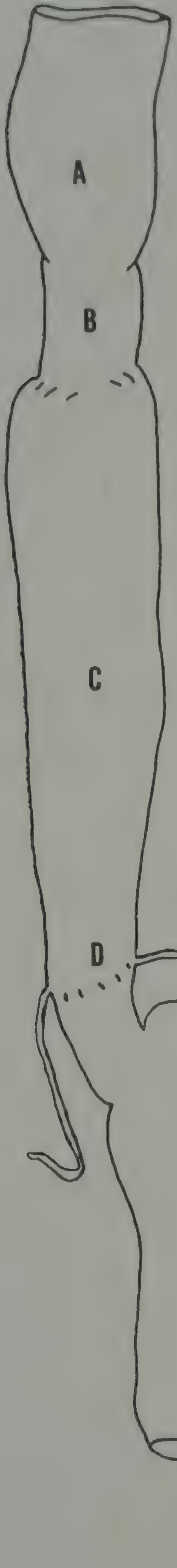
[1] Part of a study begun at the Louisiana State University under Professor J. Harvey Roberts, to whom the writer's thanks are due.

[2] *Libellula depressa* Linne, *Aeshna grandis* Linne.

[3] Schneider, 1890, *Aeshna* sp.; Sadones, 1896, *Libellula depressa* Linne.

[4] *Synthemis eustalacta* (Burmeister), *Cordulephya pygmea* Selys, *Petalura gigantea* Leach, *Hemigomphus heteroclitus* Selys, *Anax papuensis* Burmeister, *Austroaeschna multipunctata* Martin.

[5] Whedon, 1919: Considered the general types of proventricular armature of *Anax* and of the Libellulines, but gave no drawings. Fraser, 1925: *Orogomphus atkinsoni* Selys and *Orogomphus campioni* Fraser. Calvert, 1927: Stated that the armature of *Orthemis ferruginea* Fabricius and *Erythemis plebeja* Burmeister resembled Ris' (1896) figure of *Cordulia* sp. Barnard, 1937: *Mesogomphus cognatus* (Rambur), *Anax imperator* Leach, *Presba venator* Barnard, and *Pseudomacromia torrida* Kirby. Mentioned that armature of *Ceratogomphus pictus* Selys is similar to that of *Mesogomphus*; *Macromia picta* Selys is similar to that of *Presba*; that the genera *Crocothemis*, *Helothemis* have armatures strongly resembling that of *Orthetrum*. Barnard, 1940: *Pantala flavescens* Fabr. Tillyard and Fraser, 1938–1940: unidentified *Austrogomphus*, *Aeshna* and *Chlorogomphus* species. Balfour-Browne, 1944: *Aeshna* sp. and *Sympetrum* sp.



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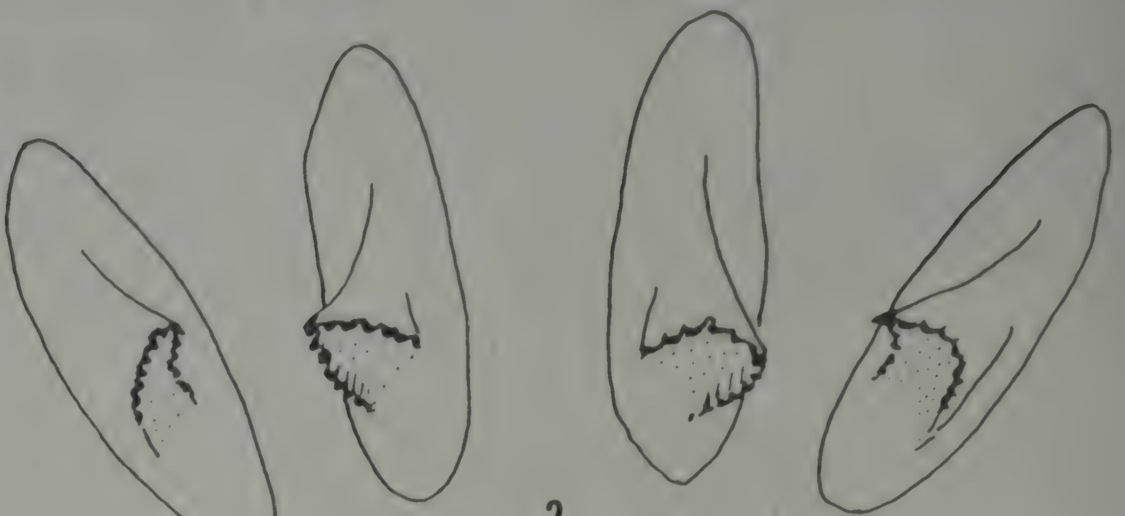

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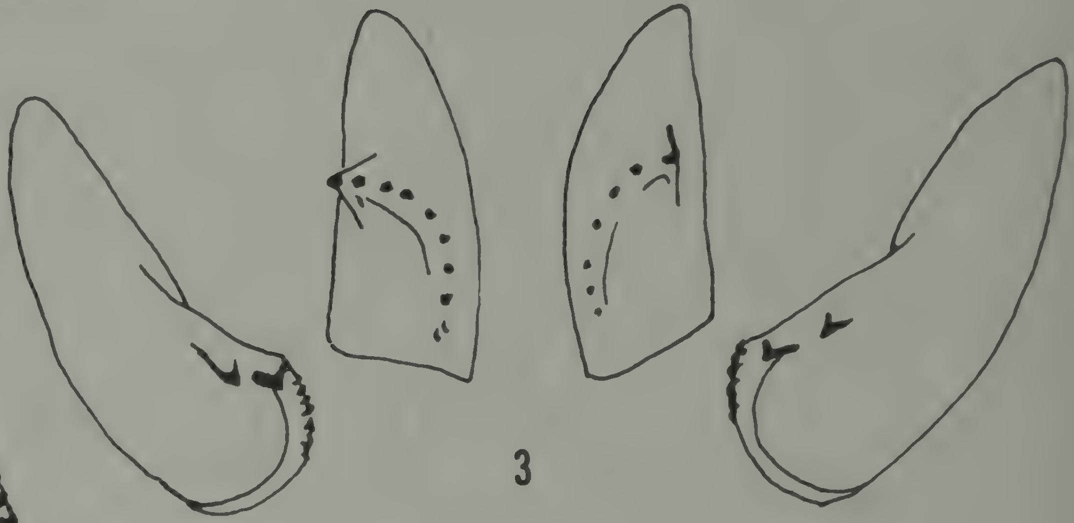

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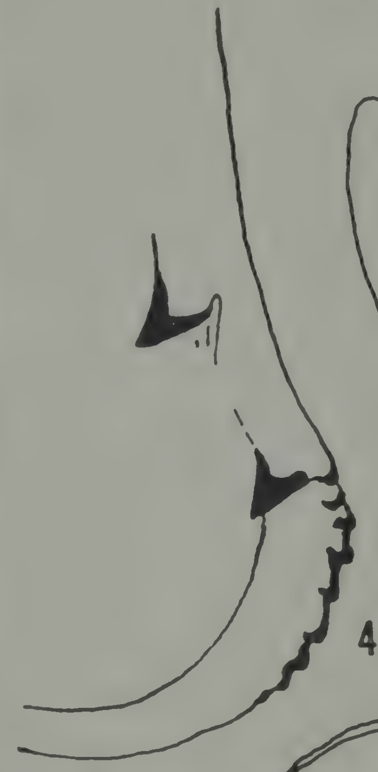

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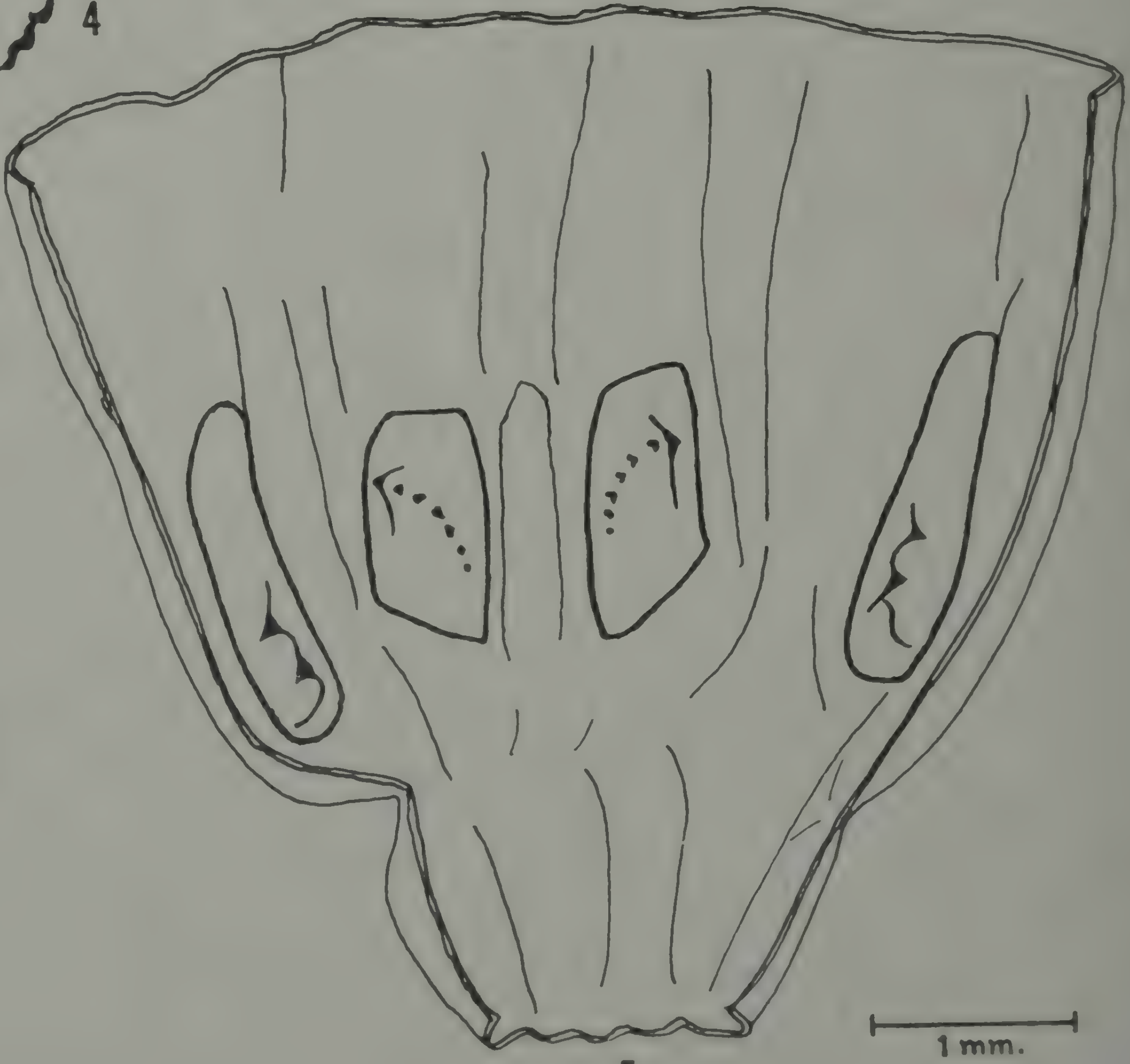

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Figs. 2–19 are camera lucida drawings made from dissections of preserved material. Of these, all but Fig. 4 are in proportion to the accompanying millimeter scales.

Fig. 1. Schematic diagram of alimentary canal of an anisopterous larva, showing location of proventriculus. A, Crop; B, Proventriculus; C, Ventriculus; D, Malpighian tubules; E, Proctodaeum. Fig. 2. Proventricular armature of *Cordulegaster maculatus;* dorsal plates in center, ventral plates in lateral position. Fig. 3. Proventricular armature of *Didymops transversa;* dorsal plates in center, ventral plates in lateral position. Fig. 4. *Didymops transversa:* view of ventral plate enlarged to show dentition of lateral margin. Fig. 5. Proventriculus of *Plathemis lydia*, opened ventrally to show plates *in situ.*

The proventriculus of the odonate larva is the part of the digestive canal connecting the crop and mid-gut and is located in the posterior thoracic region (Fig. 1). It is provided with a medial armature consisting of sclerotized areas on the longitudinal folds and is distinctly dissimilar in different families.

The most generalized type of armature, according to Tillyard (1917), is characteristic of *Petalura gigantea* Leach, of Australia, which has eight spine-bearing folds, while all other Anisoptera studied have only four. This suggests a closer relationship with the sub-order Zygoptera in which eight or more such folds are always present. The other primitive type of proventricular armature is characteristic of the family Gomphidae (Figs. 6–11). Further families (Aeshnidae and Cordulegasteridae) generally considered to be of early origin on the basis of so-called "primitive" external morphological characters differ sharply from the gomphid type

Specialization in families of Anisoptera occurring in North America has been found to proceed in several directions. From the apparently primitive gomphid type (Fig. 6) of proventriculus armed with simple sclerotized areas bearing posteriorly-directed spines, there appears to have developed the aeshnid type (Figs. 12–19) having elevated sclerotized areas with spines localized around a conical apex. Further specialization has resulted in the armature characteristic of the Cordulegasteridae (Fig. 2), in which the sclerotized areas are clearly differentiated into dissimilar dorsal and ventral pairs, each area bearing, posteriorly, two diverging dentate ridges.

Specialization reaches its ultimate development in the families Corduliidae and Libellulidae, which are believed to be the most advanced of all Odonata. In these two families, with one exception discussed later in the present paper, the sclerotized areas again occur in dissimilar dorsal and ventral pairs, but have lost the dentition on one of the ridges of the dorsal plates and on both ridges of the ventral plates (Fig. 5).

Beginning on the level considered most primitive, nine genera of Gomphidae were studied, and in *Progomphus*, *Gomphoides*, *Aphylla*, *Hagenius*, and *Dromogomphus* generically diagnostic proventricular characters were found (Figs. 6–11). These characters consist of what are now designated "minor reversed spines," a hitherto undiscovered character which may be well-developed, rudimentary, or absent; the profile and degree of elevation of the major spine-bearing area; and the number and arrangement of spines. However, in the genera *Gomphus*, *Ophiogomphus*, *Erpetogomphus* and *Octogomphus*, the species studied showed no proventricular characters that are clearly diagnostic generically.

Next in order of apparent specialization is the family Aeshnidae, of which species belonging to seven genera were studied (Figs. 12–19). In the genera *Boyeria* and *Basiaeschna* generically diagnostic characters were found, and the four genera *Epiaeschna*, *Aeshna*, *Coryphaeschna*, and *Nasiaeschna*, though showing no clear differences *inter se*, were found to have characters in common that separate them from the others. The generically diagnostic proventricular characters of the foregoing distinct aeshnid genera consist of differences in size and distribution of spines on the conical proventricular plates as well as the shape of these plates themselves.

A most interesting discovery in this study of the Aeshnidae is that two species of the important genus *Anax*, *amazili* and *junius*, show greater diversity in structure of the proventricular armature *inter se* than occurs between several other genera of Aeshnidae examined (Figs. 12–19).

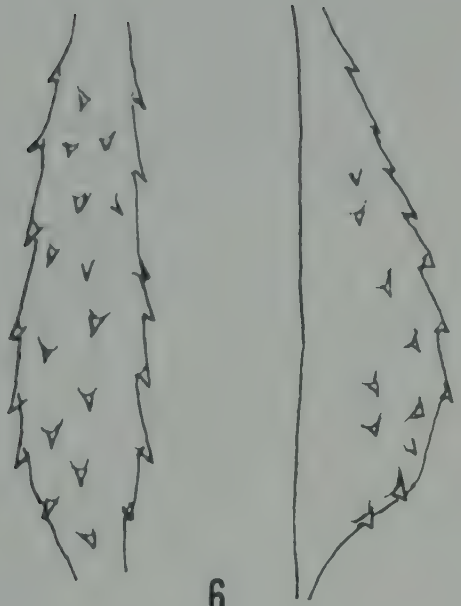
In the family Cordulegasteridae proventricular study did not progress to generic differentiation because the structure of only the holarctic genus *Cordulegaster* was investigated. On the family level the Cordulegasteridae show abrupt discontinuity from all other Odonata on the basis of proventricular characters already discussed.

Far more specialized than families so far discussed are the Corduliidae and Libellulidae, but, in the nineteen genera studied[6], among their specializations in common is the loss of proventricular characters diagnostic on either the family or genus level. However, in the case of one subfamily of Corduliidae, the Macromiinae, differentiation of proventricular structure from other Corduliidae and Libellulidae is sufficiently extreme that the separation of the Macromiinae on the family level is suggested (Figs. 3–4). The dentate lateral ridges

[6] *Didymops, Macromia, Tetragoneuria, Epicordulia, Somatochlora, Neurocorulia, Erythemis, Lepthemis, Libellula, Plathemis, Orthemis, Sympetrum, Pachydiplax, Dythemis, Brechmorhoga, Perithemis, Paltothemis, Pantala, Tramea.*

of the ventral pair of sclerotized plates are not found in any other Nearctic Corduliidae or Libellulidae.

The structure of the proventricular armature in the larvae of Odonata-Anisoptera is a taxonomic character of variable usefulness. Greater inter-generic differentiation in the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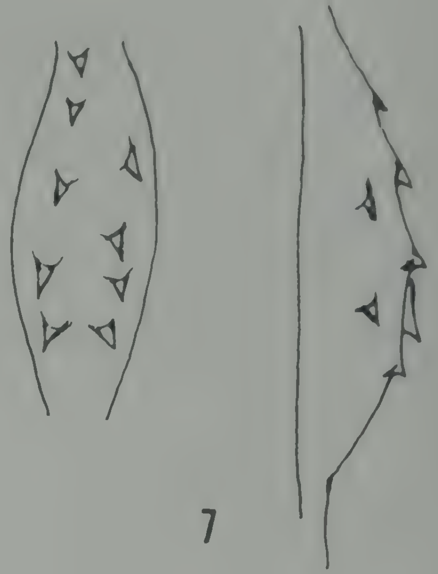
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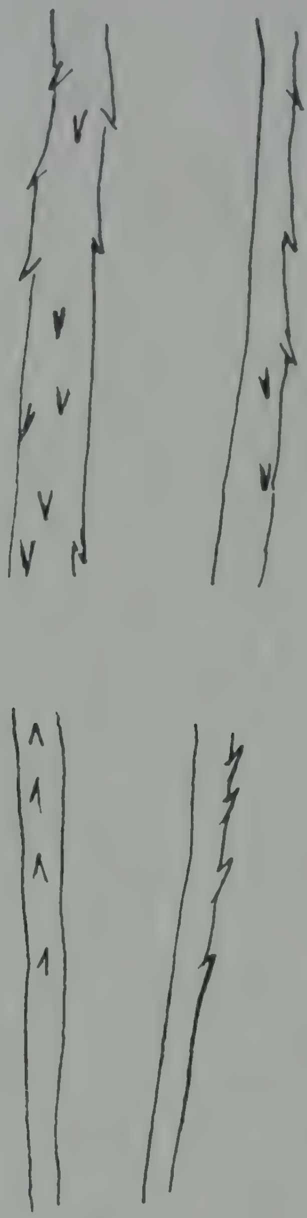
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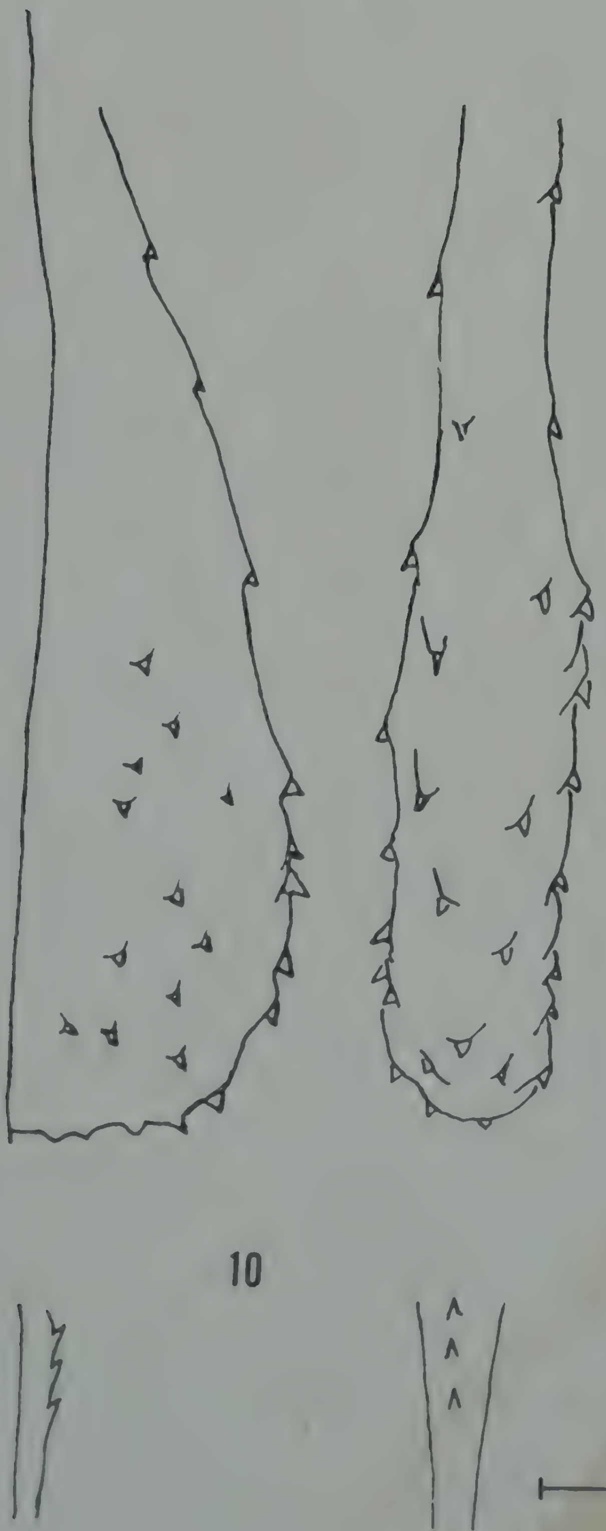
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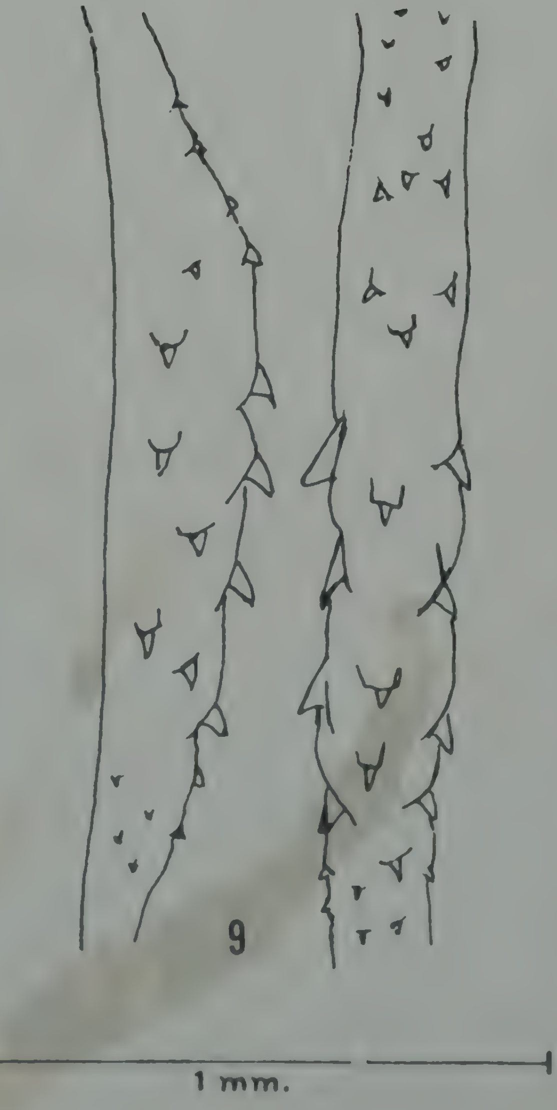
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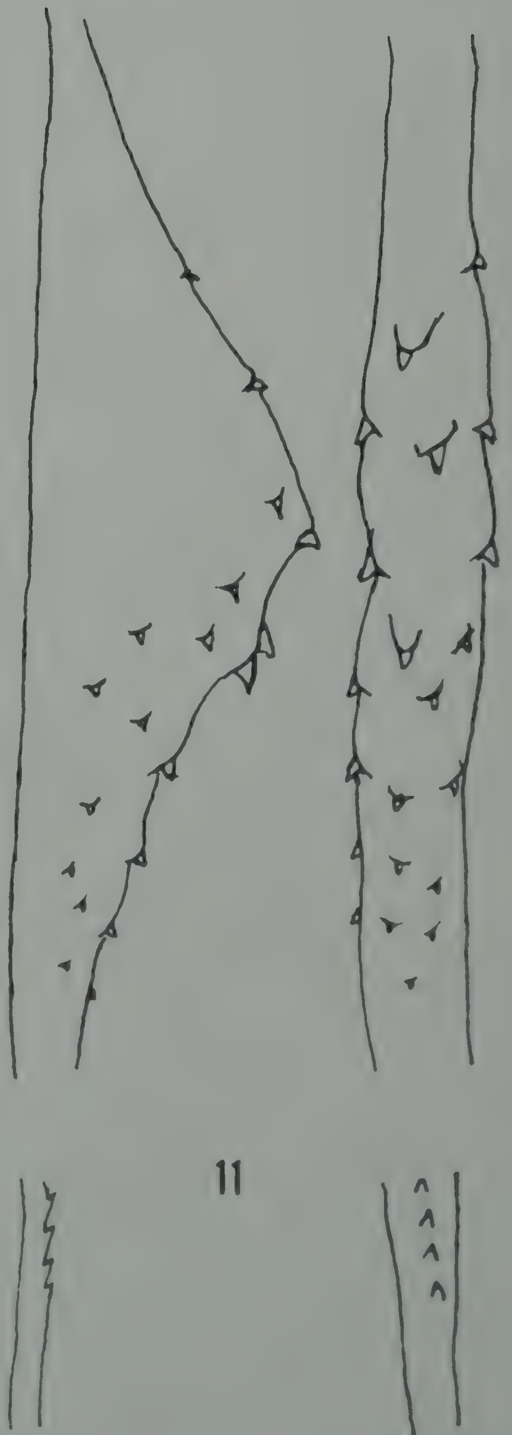
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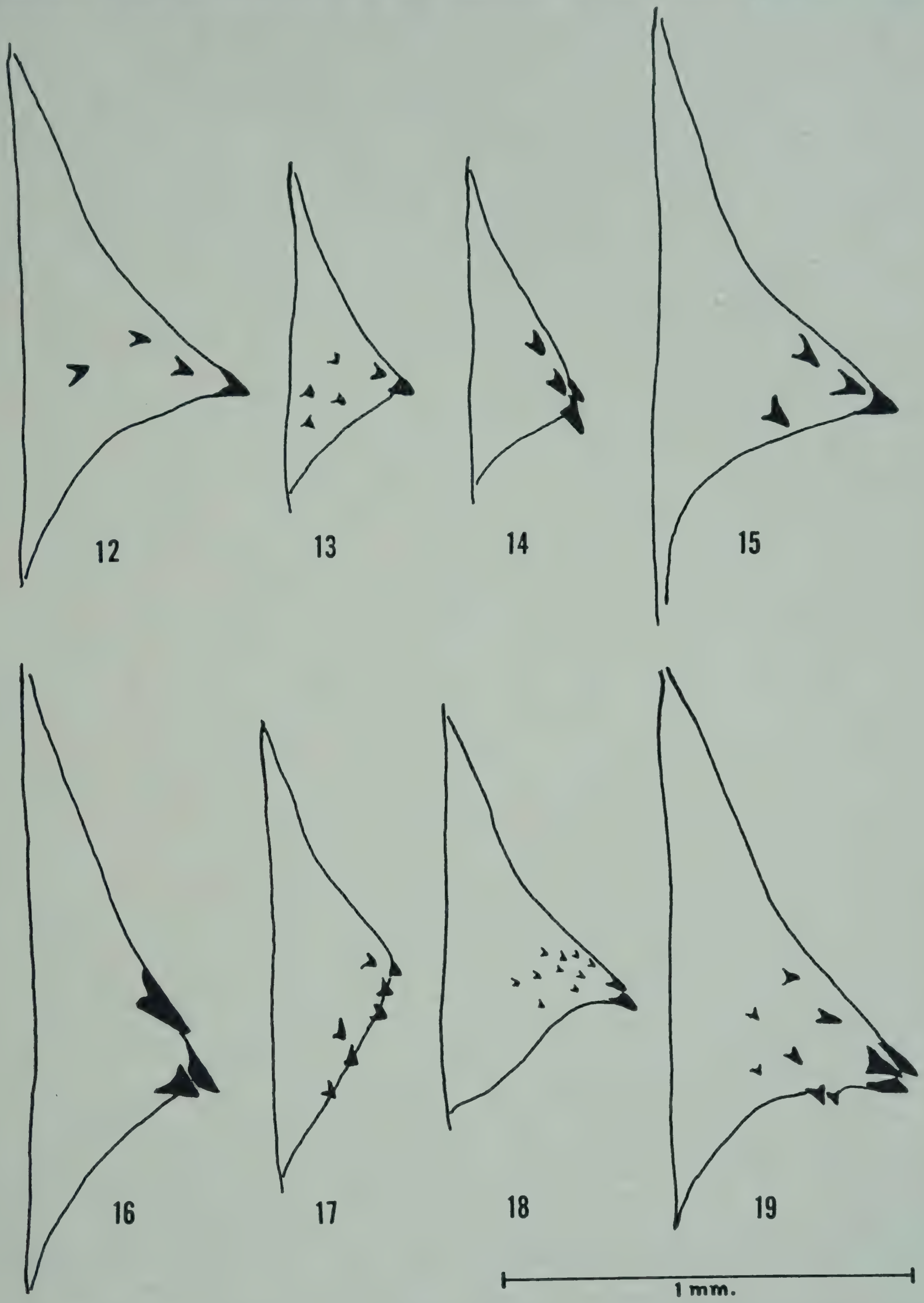
more primitive families Gomphidae and Aeshnidae make this character diagnostically useful on this level in many cases but not in all. As greater specialization is attained, proventricular structure loses its usefulness in the differentiation of genera of the Libellulidae but has been found valuable in the clarification of family distinctions not hitherto properly understood.



Figs. 12–19. Lateral views of proventricular plates of: Fig. 12, *Epiaeschna heros*. Fig. 13, *Aeshna umbrosa*. Fig. 14, *Boyeria vinosa*. Fig. 15, *Coryphaeschna ingens*. Fig. 16, *Nasiaeschna pentacantha*. Fig. 17, *Basiaeschna janata*. Fig. 18, *Anax junius*. Fig. 19, *Anax amazili*.

Note that the number and arrangement of spines and teeth on the sclerotized plates is not constant in an individual, and that the following figures (6–19) represent only the single plate under actual examination.

Figs. 6–9. One proventricular plate and lateral view of same. Fig. 6, *Gomphoides stigmatus*. Fig. 7, *Hagenius brevistylus*. Fig. 8, *Progomphus obscurus*. Fig. 9, *Dromogomphus spoliatus*, lateral view on left.

Figs. 10–11. One proventricular plate of *Aphylla williamsoni*, with lateral view on left. Fig. 10, dorsal plate. Fig. 11, ventral plate.

In Figs. 8, 10 and 11 the space between the upper and lower parts of the figures represents the actual position and size of the non-sclerotized region between the major spine-bearing areas and the small, lightly sclerotized areas bearing the minor reversed spines.

REFERENCES

Balfour-Browne, F. 1944. The proventriculus of the Coleoptera (Adephaga) and other insects—a study in evolution. *J. Roy. Microscop. Soc.* 64: 68–117.

Barnard, K. H. 1937. Notes on dragonflies (Odonata) of the S. W. Cape, with descriptions of the nymphs, and of new species. *Annals S. African Museum* 32(3): 169–260.

Barnard, K. H. 1940. Additional records and descriptions of new species, etc. *Annals S. African Museum* 32 (6): 609–661. (Odonata, pp. 659–661.)

Calvert, Philip P. 1927. Report on the Odonata, including notes on some internal organs of the larvae, collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. *Univ. Iowa Studies Nat. History* 12 (2): 3–44.

Dufour, Leon. 1852. Etudes anatomiques et physiologiques, et observations sur les larves des Libellules. *Ann. Sci. Nat.*, 3e Serie, Tome 17: 65–110.

Fraser, F. C. 1925. The true position of the genera *Orogomphus* and *Chlorogomphus* as demonstrated by a study of the larvae of *O. atkinsoni* and *O. campioni* and a comparison of the latter with the larva of *Anotogaster nipalensis* (Odonata). *Rec. Ind. Mus.* 27: 423–429.

Ris, F. 1896. Untersuchung uber die Gestalt des Kaumagens bie den Libellen und ihren Larven. *Zool. Jahrb. Jena* (Syst.) 9: 596–624.

Sadones, J. 1896. L'Appareil digestif et respiratoire larvaire des Odonates. *La Cellule* 11: 273–325.

Schneider, Anton. 1890. Uber den Darmkanal der Arthropoden. Zoologische Beitrage. Herausgegeben von Dr. Anton Schneider, II, Breslau, J. U. Kerns Verlag (Max Muller). 82–96.

Tillyard, R. J. 1910. Monograph of the genus *Synthemis*. *Proc. Linnean Soc. New South Wales* 35: 312–377.

Tillyard, R. J. 1917. The biology of dragonflies. *Cambridge University Press*, 1–396.

Tillyard, R. J., and F. C. Fraser. 1938–1940. A reclassification of the order Odonata based on some new interpretations of the venation of the dragonfly wing. (by R. J. Tillyard, with notes, preface and completion thereof, by F. C. Fraser). *Aust. Zool.* 9: 125–169, 195–221, 359–396.

Whedon, A. D. 1919. The comparative morphology and possible adaptations of the abdomen in the Odonata. *Trans. Am. Ent. Soc.* 44: 373–437.

DISCUSSION

B. I. BALINSKY. Have you any information concerning the value of the proventriculus in the classification of the Zygoptera?

A. FERGUSON–BEATTY (MRS.). I have done no work on the proventriculus of the Zygoptera. In the early part of this century, Higgins studied the proventriculus of adult Zygoptera but reached no conclusions of great taxonomic interest.

The Strepsiptera Parasitic on Heteroptera

By Teiso Esaki and Syoiti Miyamoto
Kyushu University
Fukuoka, Japan

ABSTRACT

The authors found that the cydnid bug Macroscytus japonensis *Scott was frequently parasitized by a strepsipteron in Japan. Study revealed that the bug was infected by the parasite to a high degree in certain localities. The authors obtained series of adults and immature stages of the parasite, which is an undescribed species of* Triozocera *Pierce, a genus hitherto known from the male only of a single North American species. The authors compare the new species with other Strepsiptera that parasitize Heteroptera. The results may be summarized as follows. (1) The species is described as* Triozocera macroscyti *n. sp.; descriptions are given of the adults, pupae, and mature larvae of both sexes and of the triungulin. (2) The biology is described briefly. (3)* Triozocera *is allied to the other genera that parasitize Heteroptera,* Callipharixenos, Chrysocorixenos, *and* Corioxenos, *which constitute a family, the Callipharixenidae, which has some affinities with the Mengeidae in which* Triozocera *has hitherto been placed.*

The Strepsiptera parasitic on Heteroptera are few in number of species, as compared with those parasitizing Hymenoptera or Homoptera. The authors recently discovered in Japan that the cydnid bug, *Macroscytus japonensis* Scott, was frequently parasitized by a strepsipteron of the genus *Triozocera* Pierce, which has been known only from a single North American species, *Triozocera mexicana* Pierce. The American species is known only from the male adult, and its host is unknown. We succeeded in obtaining a long series of adults and various immature stages of both sexes, including the triungulin or first larva, of the Japanese form, which may be described as a new species.

Triozocera macroscyti sp. nov.

Male (Figs. 1–5): Brownish; head and eyes blackish, antennae, mandibles, and maxillae darker brown; thorax dark brown, fore wings dark, hind wings entirely infuscate with dark brown veins, legs with tibiae and basal three tarsal segments darker, distinctly paler on apical two segments; abdomen dark brown, membranous parts paler.

Head transverse, shorter than one-half of the width including eyes, vertex with a pair of large oval lobes; eyes of raspberry appearance, each eye composed of 20 or 21 facets, inter-facettal space distinctly pubescent, antennae seven-segmented, first and second segments short, third and fourth each produced into a long branch, fifth to seventh thinner, the relative lengths of last three segments variable, the fifth may be the longest and subequal to or longer than sixth and seventh together, but sometimes the fifth and seventh subequal in length and the sixth much shorter; mandibles reduced to tiny pieces, not filamentous, maxillae single segmented, elongate and with a one-jointed palp in the middle, the palp is narrowed towards apex and extending far beyond the tip of maxilla.

Pronotum very short, one-half as broad as head; mesonotum with distinct praescutum; metanotum well-developed, each side of anterior lobe (praescutum) reaching parapteron, lateral lobes (scutum) separated by triangular central lobe (scutellum) from each other, scutellum (postscutellum) somewhat shorter than a half length of metanotum. Wings minutely pubescent, venation as shown in Fig. 1, essentially as in *mexicana*. Legs: Coxae subcylindrical except for hind coxae which are somewhat flattened, femora, tibiae and basal three tarsal segments cylindrical, fourth segment lobate, the fifth spindle-shaped, fourth and fifth much less chitinized than the preceding segments, terminal claws paired but feeble. Relative lengths of the leg segments as follows:

	Coxa	Femur	Tibia	Tarsus 1	T_2	T_3	T_4	T_5
Fore leg	50	52	49	36	16	14	10	11
Middle leg	48	52	44	33	15	14	8	9
Hind leg	23	54	50	36	16	14	10	11

100 units = 1 mm.

Abdomen largely membranous on the dorsal side, second to eighth abdominal tergites small but well-defined, smallest on second segment and largest on eighth segment; abdominal

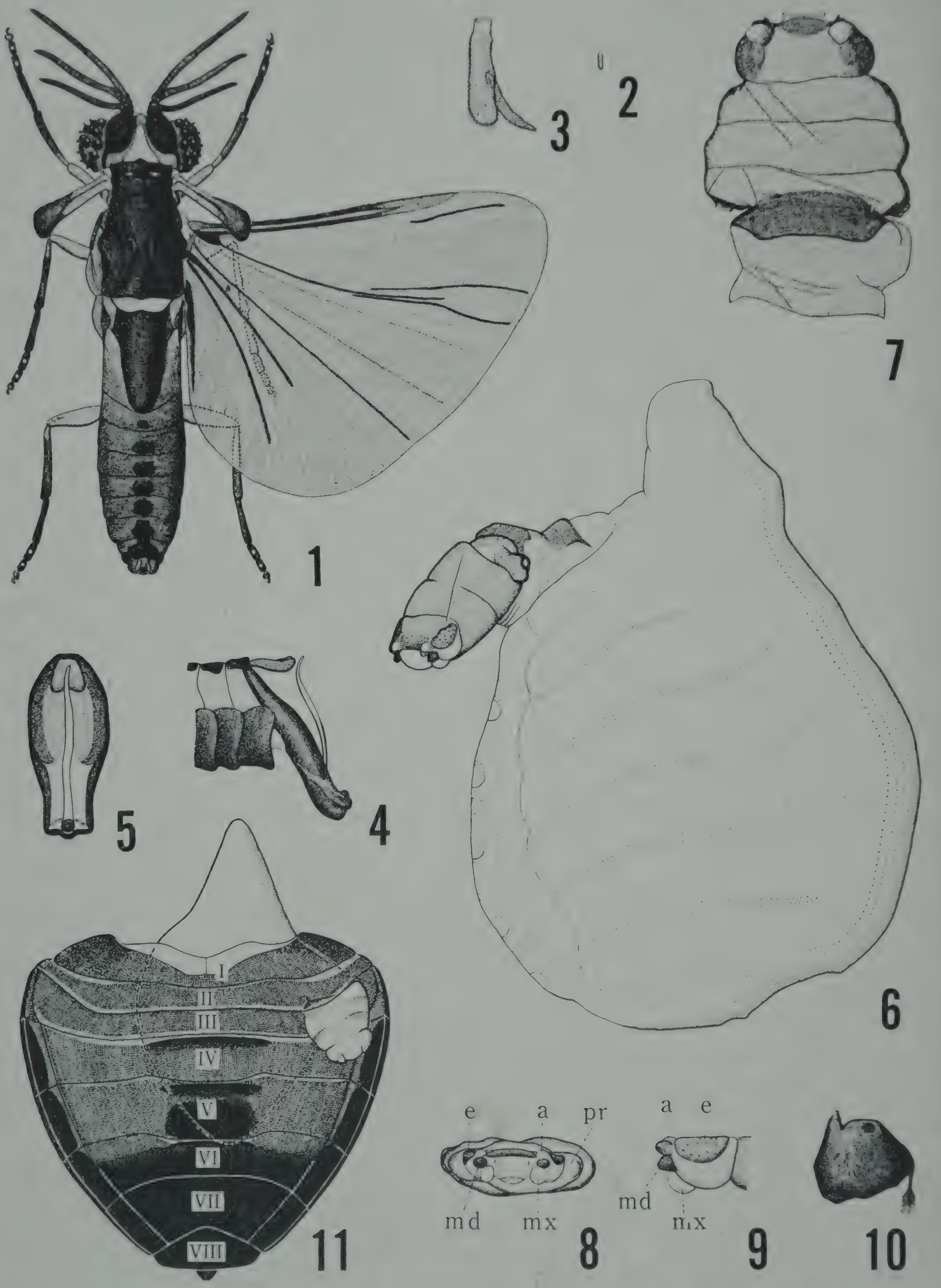


Fig. 1, *Triozocera macroscyti* sp. nov., male. Fig. 2, right-hand mandible of same. Fig. 3, right-hand maxilla of same. Fig. 4, apical abdominal segments of same, lateral view. Fig. 5, ninth abdominal segment of same with anal flap, seen from behind. Fig. 6, female, lateral view. Fig. 7, cephalothorax and first abdominal tergite of same, dorsal view. Fig. 8, head of same, frontal view. Fig. 9, head of same, lateral view. Fig. 10, right-hand mandible of female, dorsal view. Fig. 11, Adult female in abdomen of *Macroscytus japonensis* Scott, (♀). Cephalothorax protruded from between second and third abdominal tergites of host.

a, antenna; e, eye; md, mandible; mx, maxilla; pr, prothorax. Roman figures denote the abdominal segments.

sternites well-developed, first and second sternites completely fused together in the middle; genital segment (ninth) short but prolonged downwards, more or less oval in caudal aspect, aedeagus long, narrowed in the middle, with acute apex and arcuate in profile; anal segment (tenth) flap-like and truncate at apex.

Male pupa (Figs. 12–13): Brownish on cephalothorax of puparium, whitish or dark coloured adult body visible through both the pupal skin and puparium.

Pupa enclosed in larval skin (puparium). Cephalothoracic portion of puparium more or less sclerotised, head distinct from thorax, with rudiments of appendages; thoracic segments fused into a mass, segmentation scarcely recognizable, thorax with three pairs of vestigial larval legs and the pair of metathoracic spiracles. Head of pupa located on first abdominal segment of puparium, which is not projected out from the host body *in situ*; antennae very thick and with long branches on third and fourth segments, clypeus on the large frontal sac, maxillae sac-like and with a postero-ventral prolongation which may represent the palp; appendages of thorax well-developed but relatively simple and thick; ninth abdominal segment comparatively large, tenth segment small and flap-like.

Body axis of pupa in the host parallel to that of the host bug.

Male larva (Figs. 14–17): Whitish, more or less flattened dorso-ventrally, elevated along dorsal median line but quite flat on ventral side. Head with rudiments of eyes, antennae, mandibles, and maxillae, median frontal sac representing clypeal region, genal part differentiated between eye and mandible. Thorax distinctly three-segmented, with a pair of vestigial legs on each segment; rudiments of pupal wings and legs, formed under larval skin, may be recognizable externally; abdomen ten-segmented, first three segments each with a dorsal, median, fleshy projection near posterior margin, the following four segments more or less elevated dorsally near posterior margin, ninth segment produced dorsally.

At the end of larval stage, the head becomes more or less chitinized on interspace of eyes, on genae, and on mandibles, antennae clearly bordered from eyes, and metathoracic spiracles formed. Form of pupal appendages evident, and the anterior part of the body before first abdominal segment slightly bent ventrally.

Body length: 3.5-3.9 mm. Greatest width. 1.3 mm. Greatest height: 0.8 mm.

Female (Fig. 6–10): Cephalothorax somewhat yellowish and abdomen whitish. Larviform, sac-like. Cephalothorax more or less asymmetrical, almost as wide as long (91:87), segmented and recurved on ventral surface of abdomen and projected from the host on its dorsal side of abdomen (Fig. 11); head slightly narrower than prothorax and with vestigial appendages, ocular region recognizable, with obscure, tiny facet-like structures, antennae pale and detectable, low tubercles before eyes, mandibles well-chitinized, with a tooth at inner angle, maxillae less chitinized and larger than mandibles, opening of brood chamber between maxillae. Pro- and mesothorax without special structure, metathorax subequal in width to mesothorax and with a pair of spiracles near posterior angles.

Abdomen pear-shaped as a whole, ten-segmented; first segment small, short, more or less chitinized dorsally and united with metathorax, second segment the largest segment, with a large, dorsal, fleshy projection which is *in situ* directed to head of the host, segmentation of abdomen behind the second segment obscure, second to eighth segments recognized by obscure fuscate bands; openings of genital tubes fine, on third to seventh abdominal segments.

Body length, from tip of fleshy projection on second abdominal segment to the apical end: about 4.5 mm. Greatest width of cephalothorax: 0.9—1.0 mm; the same of abdomen: 1.2—1.3 mm.

Female larva (Fig. 18–19): Whitish, with fuscate band on lateral portion of each abdominal segment except for tenth segment.

Body much more swollen dorsally than in male larva. Cephalothorax distinctly segmented; head not only with rudiments of mandibles but of eyes, antennae, and maxillae, clypeus as in male larva; rudiments of eyes and antennae fused with each other and not differentiated from genal part, mandibles relatively smaller than those in younger larvae, maxillae without indication of palp. Thoracic appendages entirely wanting, metathoracic spiracles appearing at the end of larval stage.

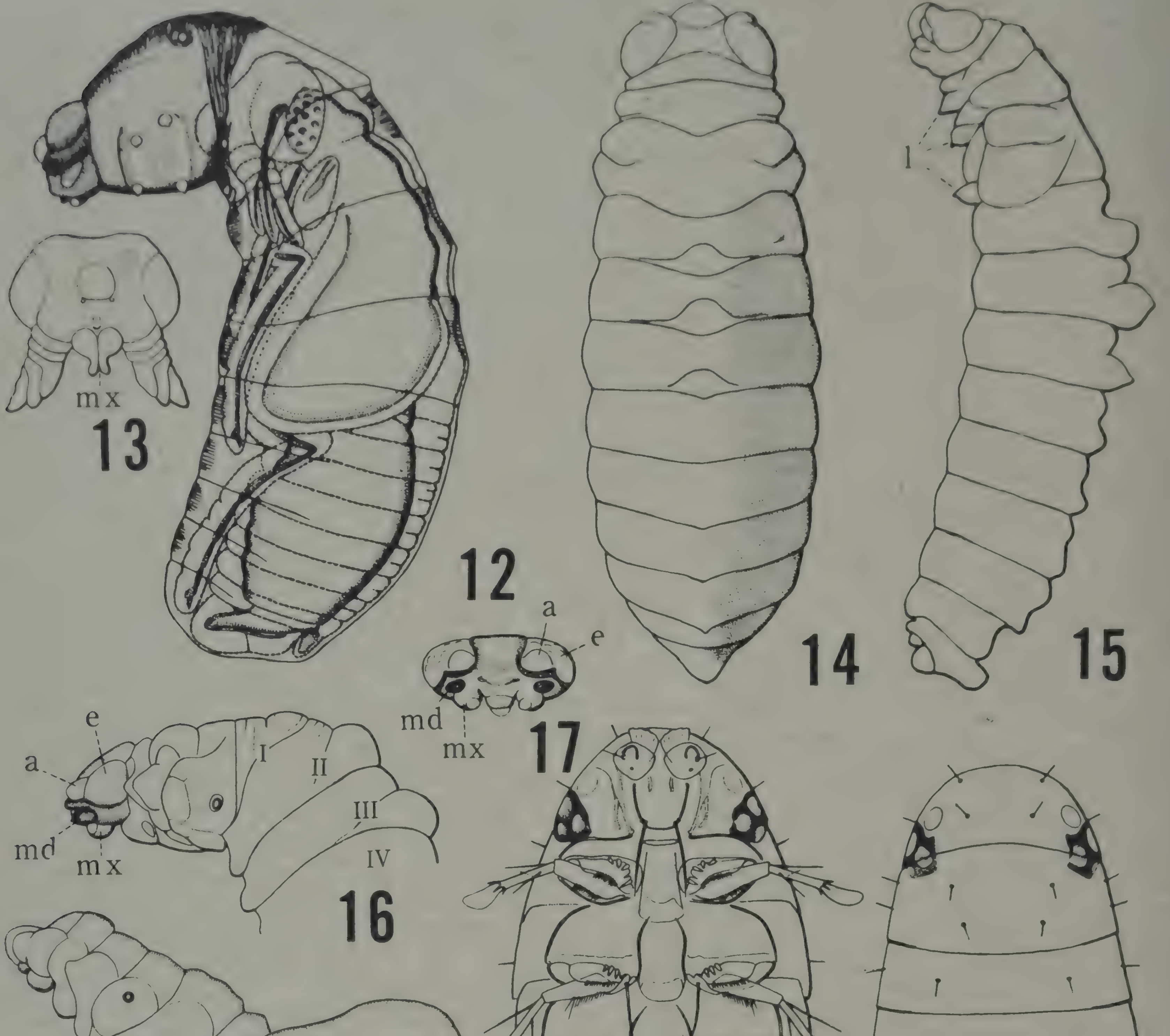


Fig. 12, Male pupa (thicker broken line) of *Triozocera macroscyti* sp. nov. in puparium, adult insect is formed within pupal skin, lateral view. Fig. 13, head of pupa, frontal view. Fig. 14, premature second larva of male, dorsal view. Fig. 15, the same, lateral view. Fig. 16, anterior part of mature second larva, lateral view. Fig. 17, head of the same, frontal view. Fig. 18, mature second larva of female, lateral view. Fig. 19, cephalothorax of the same, frontal view. Fig. 20, first larva, dorsal view, drawn from the specimen mounted in balsam without being treated with KOH. Fig. 21, the same, ventral view, drawn from the specimen mounted with glycerin after treatment with KOH.

l, rudimentary leg; other abbreviations as in Figs. 1–11.

Abdomen ten-segmented, flattened ventrally; first segment small, continuous to narrower metathoracic segment, second segment largest and with a median, dorsal, fleshy projection, the following segments gradually diminishing in size towards apex, seventh to ninth segments with a median, posterior elevation on dorsal side, tenth segment very small. A median pit, showing the position of opening of genital tube, present on the centre of third to seventh abdominal sternites.

Body length: 3.7-4.5 mm.

First larva or triungulinid (Figs. 20–21): Brownish yellow and ellipsoid in outline. Head with three pairs of bristles on dorsal side of which one pair is before eyes and on lateral margins; eyes composed of three ocelli and located in a dark patch, antennae circular, not segmented and situated before eyes, mandibles subtriangular, lobe-like, maxillae lobe-like, circular in outline, with a distinct bristle near outer margin, labium large and with a pair of long bristles at posterior angles.

Pronotum longest on median line with four pairs of bristles of which two pairs are situated on the lateral margins, lateral parts of posterior margin file-like; meso- and metanota with two pairs of bristles respectively, one of the pairs on lateral margins, posterior margins file-like as on the pronotum. Ventral sternal plates between coxae not dentate on posterior margins. Legs well-developed; fore and middle legs with large, oblong, sac-like tarsi or adhesive organs, hind ones with long, bristle-like tarsi; a long bristle on the bases of middle and hind legs.

First to eighth abdominal tergites each with a bristle near lateral margin; ninth tergite much the longest, with three pairs of bristles, first pair submedian and near anterior margin, second pair on the middle of lateral margins, the third near posterior angles. Abdominal sternites much narrower than tergites. Second to eighth sternites furnished with four or five teeth on hind margin, eighth sternite with a pair of bristles, ninth sternite divided into two parts by a feeble transverse line, anterior lobe with two pairs of bristles near hind border, outer ones long and stout, tenth segment with a pair of very long bristles, which are more than three times the length of the longer bristles on ninth sternite.

Body length: 0.16–0.17 mm. in alcholic specimens. Greatest width: 0.075 mm.

Habitat: Japan (Kyushu).

Holotype ♂, emerged on May 23, 1955; allotype ♀, on May 15, 1955; and many paratypes: males, emerged from May 17 to May 23, females, from May 4 to June 27, male pupae, from April 27 to May 23, second larvae, almost through the year 1955, and first larvae, hatched on June 28–29, Kurume, Prov. Chikugo, Kyushu, S. Miyamoto leg.; 1 ♂, at light, Saga, Prov. Hizen, Kyushu, T. Hidaka leg.

Host: *Macroscytus japonensis* Scott (Cydnidae).

This species is distinguished from the American species, *Triozocera mexicana* Pierce, by the shape of cephalic oval lobes, plate-like mandibles, distinctly longer maxillary palp, relative length of tarsal segments, well-defined abdominal tergites, and by other characters.

Biological Notes

The host bug, *Macroscytus japonensis* Scott, is a common species in Kyushu, though its habitat is rather restricted. The strepsipterous parasite occurs in different localities within Kyushu but the percentage of bugs parasitized, as well as the number of parasites in a single host, varies a great deal. The following tables show examples met with at Kurume in 1955, where the parasite population was the most dense.

TABLE I. Number of Parasites in Hibernated Population (April 11—June 1, 1955).

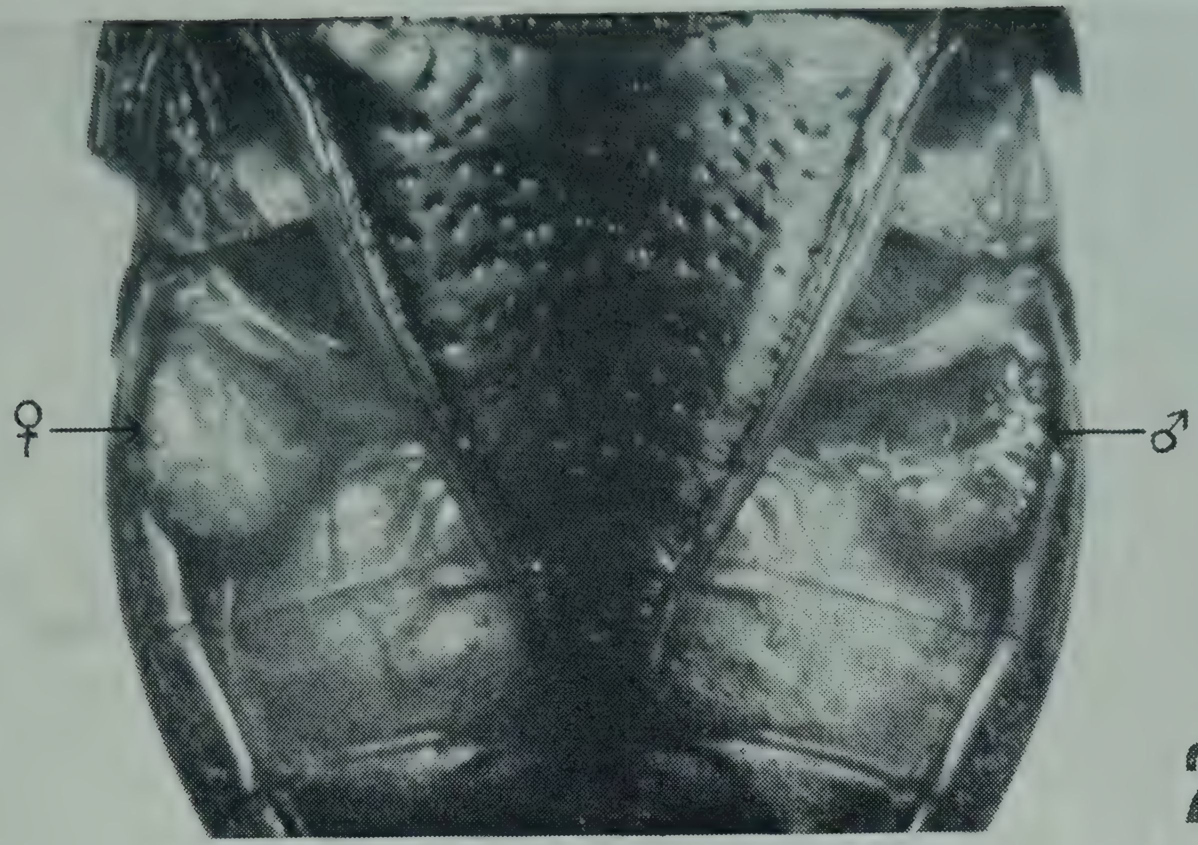
Sex of host	Number of infected bugs according to number of parasites in a single host							Number of non-infected bugs	Number of bugs examined	Parasitic percentage
	3♂♂	2♂♂ 1♀	2♂♂	1♂ 1♀	2♀♀	1♂	1♀			
♂	1	1	4	13	1	19	10	27	76	64.5
♀	1	–	5	9	–	29	19	40	103	61.2
Total				112				67	179	62.57

TABLE II. Number of Parasites in Newly Infected Population (August 11, 1955—March 17, 1956).

Sex of host	Number of infected bugs according to number of parasites in a single host												Number of non-infected bugs	Number of bugs examined	Parasitic percentage
	2♂♂ 3♀♀	1♂ 4♀♀	2♂♂ 2♀♀	1♂ 3♀♀	4♀♀	3♂♂	3♀♀	2♂♂	1♂ 1♀	2♀♀	1♂	1♀			
♂	–	1	1	–	1	1	1	2	–	1	2	1	5	16	68 8
♀	1	–	1	1	–	–	–	1	1	1	3	2	7	18	61 1
Total						23							12	34	64 12

As shown in the foregoing tables, when the parasites are in earlier larval stages, up to five parasites may be found in a single host, but when they become mature larvae, pupae, or adults (♀♀), at most three parasites only can live in a single host.

When the first larvae hatch out, crawl about, and come across the larval host, they penetrate into the body cavity of host through intersegmental membrane, and they may be found in the abdomen as well as in the thorax of the host, as ascertained by dissection. The second larvae, however, are always found in abdominal cavity, near the rectum, or beneath the posterior portion of alimentary canal. The heads of the mature larvae are directed to the front of the host. The cephalothorax of male puparium and of female adult are always exposed on the dorsal side of the host between the second and third abdominal



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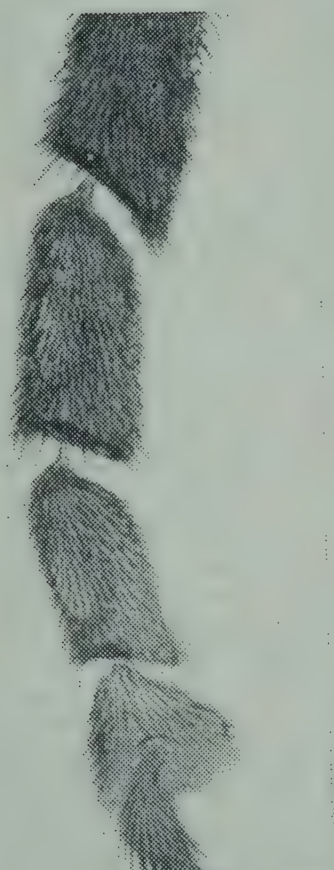

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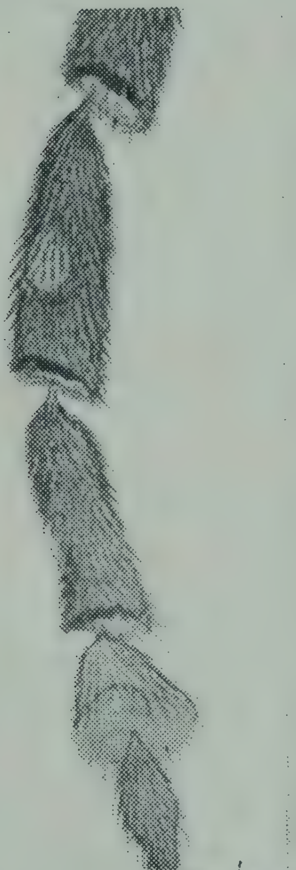

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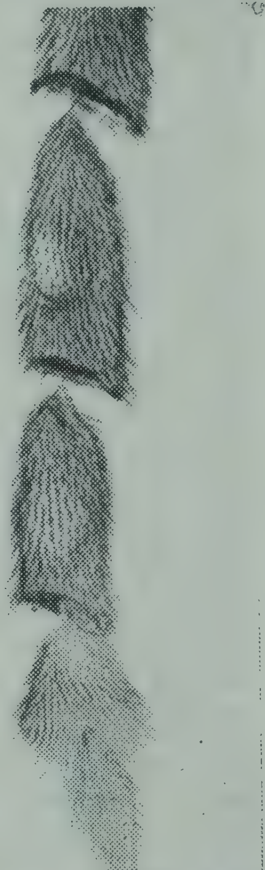

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Fig. 22, an adult female and a male puparium of *Triozocera macroscyti* sp. nov. on a single host bug, elytra and wings of the host removed. Fig. 23, apical tarsal segments of left-hand fore leg of *Triozocera macroscyti* sp. nov. Fig. 24, the same of left-hand middle leg. Fig. 25, the same of left-hand hind leg.

tergites (Figs. 11 and 22); thus the parasites are always concealed under the elytra and wings of the host, even when they are mature and partly exposed.

The effect of parasites in larval stage upon the host is indistinct, owing to the relatively minute size of the parasite, but when the host is over-infected, the effect may be too obvious. On June 28, 1955, several bugs in the second or third instar were introduced into a vial, which was crowded with first larvae of *Triozocera*, and all bugs were killed by over infection within two days; one of the bugs was carefully dissected and no less than 57 parasites were found in its body cavity.

The effect on the adult host is apparently mechanical; visceral organs of the host, especially the ovaries in female, are pressed by the parasites. The ovaries of parasitized bugs are generally depressed and mature imperfectly, but the ability of oviposition may not always be lost, for, in two cases, a female bug with a female parasite laid a few eggs, of which about a half hatched three weeks later. Copulation between parasitized bugs is often observed, but oviposition does not occur generally. No distinct effect of stylopisation can be observed.

The male adults of *Triozocera macroscyti* appear from the beginning of May and are most abundant in the latter part of the month, while the female adults began to appear some time later than the males, and the first larvae are produced at the end of June.

The oviposition of the hibernated bugs occurs from the beginning of May to the end of July; the larvae begin to hatch out near the end of May; and the newly emerged adults may be found in August.

Although male *Triozocera* and female parasites in the host bugs were often observed in captivity during the season of emergence, no copulation or searching action for a mate was observed. It is probable that the parthenogenesis may occur in the parasite, for a female of *Triozocera* reared separately, free of male parasites, produced a number of first larvae.

A detailed account of the bionomics of this interesting species will be published in a separate paper.

SYSTEMATIC POSITION

The genus *Triozocera* Pierce was placed in the family Mengeidae, by Pierce in 1909 and was based on the structure of the male tarsi, which are 5-segmented and with terminal claws. Bohart regarded the genus as most specialized of the family, though the 7-segmented antennae are more primitive than the 6-segmented ones of *Eoxenos* or *Mengenilla* of the same family.

Although males of *Triozocera* show some characters referable to mengeid genera, the tarsal structure is quite different in the apical two segments. The females are not free living as are other members of the family, *Mengenilla* and *Eoxenos*. It seems, therefore, not appropriate to rank the genus *Triozocera* within the family Mengeidae.

There are three known species of Strepsiptera that are parasitic on Heteroptera. Of these, *Callipharixenos muiri* Pierce (host: *Calliphara billiardierei* Fabricius, Pentatomidae-Scutellerinae) from Amboina and *Chrysocorixenos siamensis* Pierce (Host: *Chrysocoris grandis* Thunberg, Pentatomidae-Scutellerinae) from Siam have been known only from females extracted from dried specimens of the host bugs. The third species, *Corioxenos antestiae* Blair (Host: *Antestia lineaticollis* Stal, Pentatomidae-Pentatominae) from Tanganyika was described in detail by Blair from both sexes. He correctly pointed out the close relationship of his genus to *Triozocera* and the incorrectness of placing the latter in the same family as *Mengea*.

In the second larva of *Triozocera*, there are some affinities with Mengeidae in the presence of rudiments of eyes and of other appendages in both sexes and in the relatively flattened body in male, but the appendages are distinctly less developed than in the Mengeidae. The chaetotaxy of the first larva in *Triozocera* does not agree with that of *Eoxenos* and *Mengenilla* but is more like that of the Stylopidae, especially the chaetotaxy along lateral sides of the body; i.e., there is a single row of bristles in *Triozocera* as well as in the Stylopidae, but there are two rows in *Eoxenos* and *Mengenilla*. The antennae of *Triozocera* are normally seven-segmented, but sometimes fusion of segments occurs among the apical three segments, and this fact may indicate that the antennal characters of the two genera are not fundamentally different. The apical two tarsal segments in *Triozocera* show a tendency to reduction both in size and in chitinization, and, moreover, the lobate fourth segment is common to both the genera. General features of female adults in both genera, *Triozocera* and *Corioxenos*, are similar; both have the recurrent cephalothorax, fleshy dorsal projections on the abdominal segments, and the subtriangular, transparent windows on the sides of the head, probably corresponding to the genal region, but the head appendages differ distinctly.

There are considerable differences in the second larvae of the two genera, not only in outline but also in head and thoracic structure. The chaetotaxy of the first larva of *Corioxenos* was not shown sufficiently, but that on the ninth sternite is obviously different from that of *Triozocera* in position and length; the sternal plates between the coxae and the ninth abdominal sternite are different, but the tarsi and the second to eighth abdominal sternites are quite similarly constructed.

Thus, although there are some distinct differences, the close relationship of *Corioxenos* and *Triozocera* is obvious, and these two genera belong to one family. *Callipharixenos* and *Chrysocorixenos* are insufficiently known; the adult males are not as yet discovered, so that the relationship of those two genera to *Corioxenos* and *Triozocera* is not to be ascertained definitely. However, the asymmetrical feature of cephalothorax, small head, more or less segmented thorax, and dependence on Heteroptera suggest that those genera are all related and may constitute a family, the Callipharixenidae, which should be placed between the Mengeidae and the other families of Xenoidea.

The Callipharixenidae may be divided as follows:

1. Female with two pairs of spiracles in the cephalothorax and with five genital tubes; scutellerid parasites (males unknown) . . . . . *Callipharixenos* and *Chrysocorixenos*

   Female with a single pair of spiracles in the cephalothorax 2

2. Male with seven-segmented antennae and with five-segmented tarsi that have terminal claws; female with five genital tubes; cydnid parasites . . . . *Triozocera*

   Male with five-segmented antennae and with four-segmented tarsi that lack terminal claws; female with four genital tubes; pentatomid parasites . . . . *Corioxenos*

Recently the authors obtained another strepsipteron parasitic on lygaeid bugs of the subfamily Blissinae. The characters of the male adult show that the species may represent a very distinct new genus of the order. The report on this species will be published in a separate paper.

REFERENCES

Blair, K. G. 1936. A new genus of Strepsiptera. *Proc. Roy. Ent. Soc. London* 5: 113–117.

Bohart, R. M. 1941. A revision of the Strepsiptera with special reference to the species of North America. *Univ. Calif. Publ. Ent.* 7: 91–160.

Parker, H. L., and H. D. Smith. 1933. Additional notes on the strepsipteron *Eoxenos laboulbenei* Peyerimhoff. *Ann. Ent. Soc. Amer.* 26: 217–233.

Parker, H. L., and H. D. Smith. 1934. Further notes on *Eoxenos laboulbenei* Peyerimhoff, with a description of the male. *Ann. Ent. Soc. Amer.* 27: 468–479.

Pierce, W. D. 1909. A monographic revision of the twisted-winged insects comprising the order Strepsiptera Kirby. *Bull. U. S. Nat. Mus.* 66: 1–232.

Pierce, W. D. 1911. Strepsiptera. *Gen. Insectorum*, fasc. 121: 1–54.

Pierce, W. D. 1918. The comparative morphology of the order Strepsiptera, together with records and descriptions of insects. *Proc. U. S. Nat. Mus.* 54: 391–501.

Silvestri, F. 1941–43. Studi sugli Strepsiptera (Insecta) III. Descrizione e biologia di sei specie italiane di *Mengenilla*. *Boll. Lab. Zool. Gen. Agr. Fac. Agr. Portici* 32: 197–282.

Ulrich, W. 1927. Strepsiptera. *Biologie der Tiere Deutschlands* 41: 1–103.

Differentiation of Mosquito Extracts by their Infrared Spectra[1]

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ABSTRACT

Aqueous and carbon disulfide extracts of Aedes aegypti, A. pseudoscutellaris, Culex fatigans, C. fatigans (W), C. molestus *and* Anopheles quadrimaculatus *were prepared by homogenizing whole specimens in a tissue grinder. Following centrifugation, the clear supernate was spread on silver chloride plates. The specimens were dried at 37°C and analyzed within 24 hours of preparation. The infrared absorption spectra from 2–16 microns were determined with a Baird double-beam recording instrument equipped with a sodium chloride prism.*

The aqueous extracts of the various species could be distinguished by qualitative differences in the 6–11 micron portion of the curve. The most important differences were the relative shapes and intensities of the peaks from 6.8 to 7.1 microns and the relative depth and shape of the broad band from about 8.6 to 10.6 microns. When aqueous extracts were prepared from 7–14 day-old specimens, certain spectral changes occurred. The carbon disulfide extracts of the different species could not be differentiated consistently.

During recent years, infrared spectrophotometry has become increasingly utilized for the biochemical characterization of biological material. It has shown promise as a method for the classification or identification of bacteria (Stevenson and Bolduan, 1952; Levine *et al.*, 1953; Smith *et al.*, 1954) and viruses (Benedict *et al.*, 1954; Benedict, 1955), as well as for the chemical measurement of a variety of cellular constituents (Blount and Fields, 1948, 1949; Frazer and Chayen, 1952; Noll and Bloch, 1953; Randall *et al.*, 1949). It seemed logical, therefore, that infrared absorption techniques might be applicable to certain problems in insect taxonomy and speciation. A preliminary investigation with the aqueous extracts of three species of mosquitoes showed that they could be differentiated on the basis of certain qualitative differences in their infrared spectra (Micks and Benedict, 1953). A subsequent study of the *Culex pipiens* complex, using infrared absorption techniques, revealed reproducible differences between carbon disulfide extracts of *Culex pipiens*, *C. fatigans* and *C. molestus* (Micks and Scrollini, 1954).

Our recent studies, which are reported herein, add new information regarding the characterization of strains and species of mosquitoes by their absorption curves and the changes in the spectra that occur with age.

MATERIALS AND METHODS

All of the mosquito species used (*Aedes aegypti*, *Aedes pseudoscutellaris*, *Anopheles quadrimaculatus*, *Culex molestus* and *Culex fatigans*) were reared continuously on a standard laboratory diet, with the exception of a strain of *C. fatigans* (W) which was collected. This was obtained as fourth-stage larvae and pupae from a sewage effluent. Both aqueous and carbon disulfide extracts were prepared from a number of batches of each species at various intervals of time from one to fourteen days of age. The aqueous extracts were obtained by homogenizing 250 mg. of mosquitoes in 4 ml. of distilled water. Following centrifugation for 15 minutes at 1500 r.p.m., 0.2 ml. of the clear supernate was placed on each of two silver chloride plates. The material was distributed evenly over the area to be analyzed and allowed to dry slowly at 37°C. The plates were analyzed with a Baird double-beam recording spectrophotometer in the 2 to 16μ wave-length range. The resulting spectral curves were compared closely to discern any quantitative or qualitative differences. The carbon disulfide extracts were processed in a similar manner. The results are based upon absorption curves obtained from dozens of extracts of each species.

RESULTS

Fig. 1 shows the reproducibility of the spectra obtained from different extracts of the same species (*C. molestus*). The curves represent four aqueous extracts prepared from widely separated generations. The infrared curves (6–11μ) from extracts of 24-hour old *A. aegypti*,

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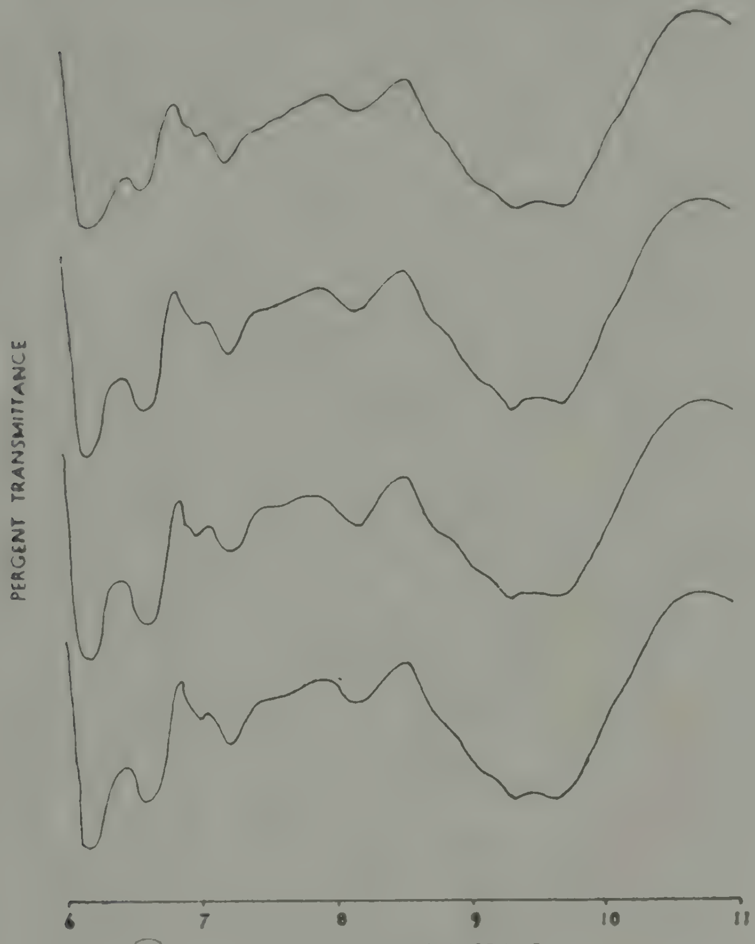
A. pseudoscutellaris, *A. quadrimaculatus*, *C. molestus*, *C. fatigans* and *C. fatigans* (W) are compared in Fig. 2. Differences between the species can be seen by comparing the shapes of the peaks between 6.8 and 7.1μ and the depth of the band at 7.2μ. *C. fatigans* and *A. quadrimaculatus*, for example, show two distinct peaks; however, the former species exhibits the deepest band (7.2μ). Likewise, there are reproducible differences in the shape of the broad band between 8.6 and 10.6μ. For example, the curve representing *A. quadrimaculatus* is comparatively straight-sloped as compared with the various culicine species. Furthermore, this broad band tends to "level off" at the bottom (between 9.4 and 9.8μ) in *C. molestus* (Fig. 1). It can be seen that the spectra obtained from *C. fatigans* and C.



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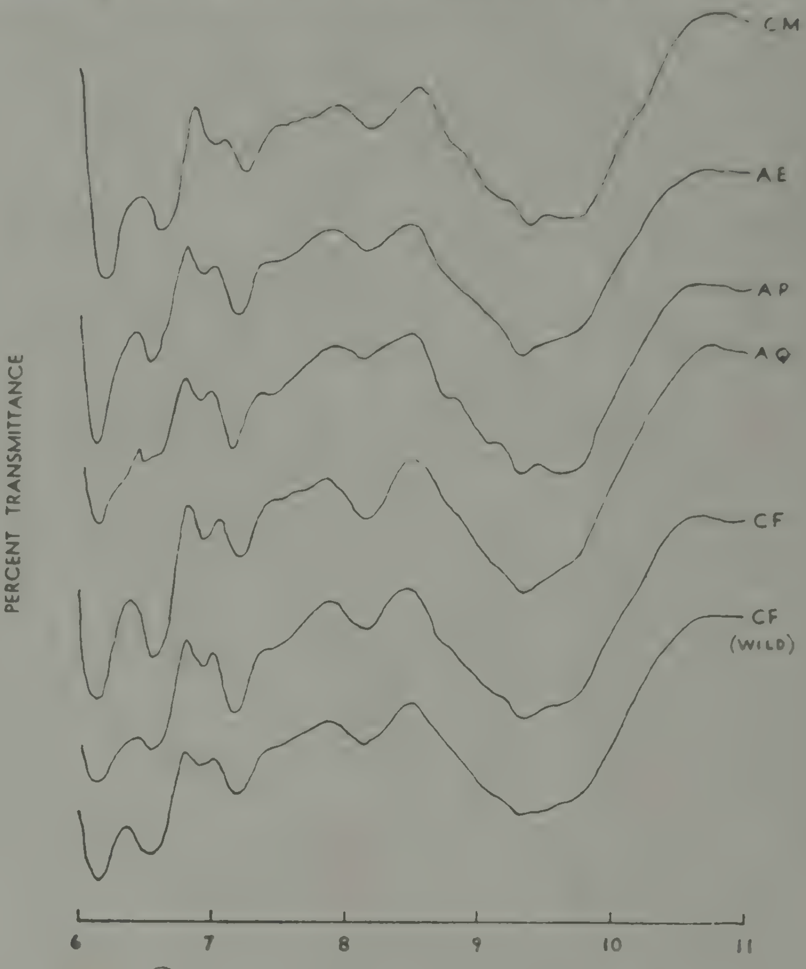

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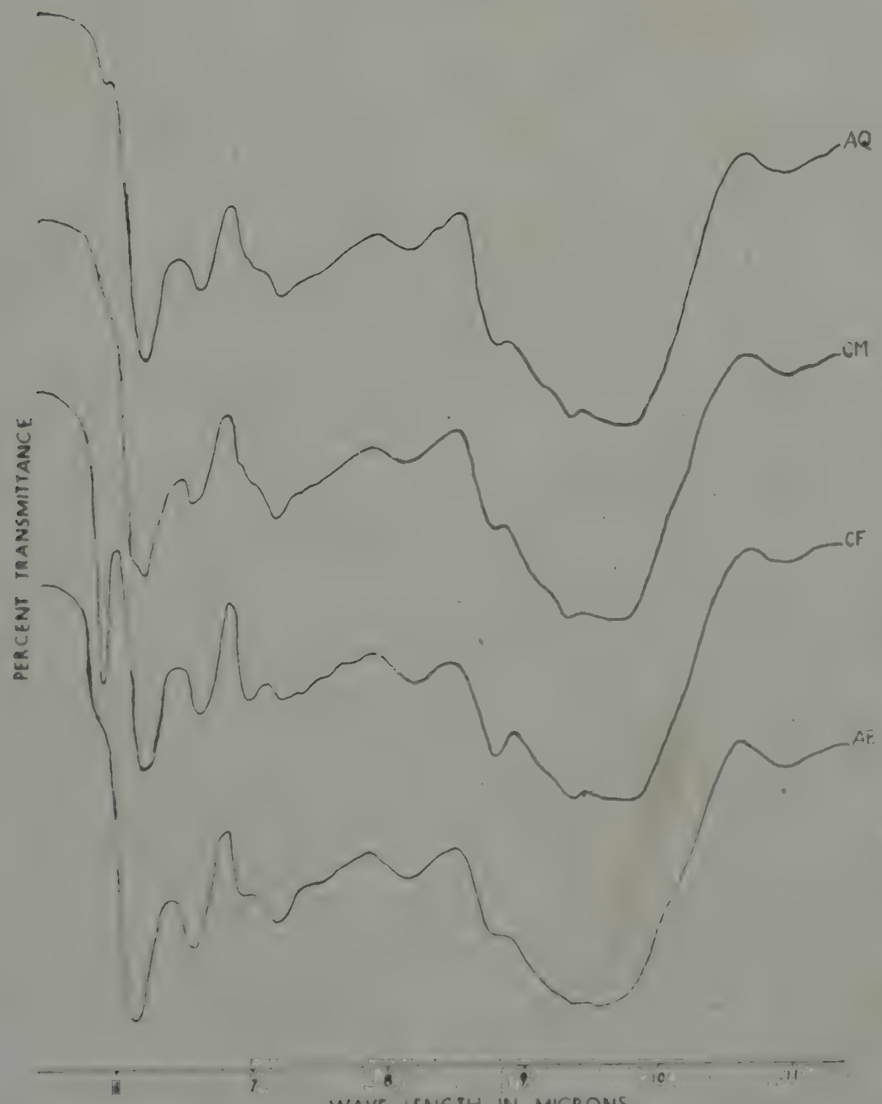

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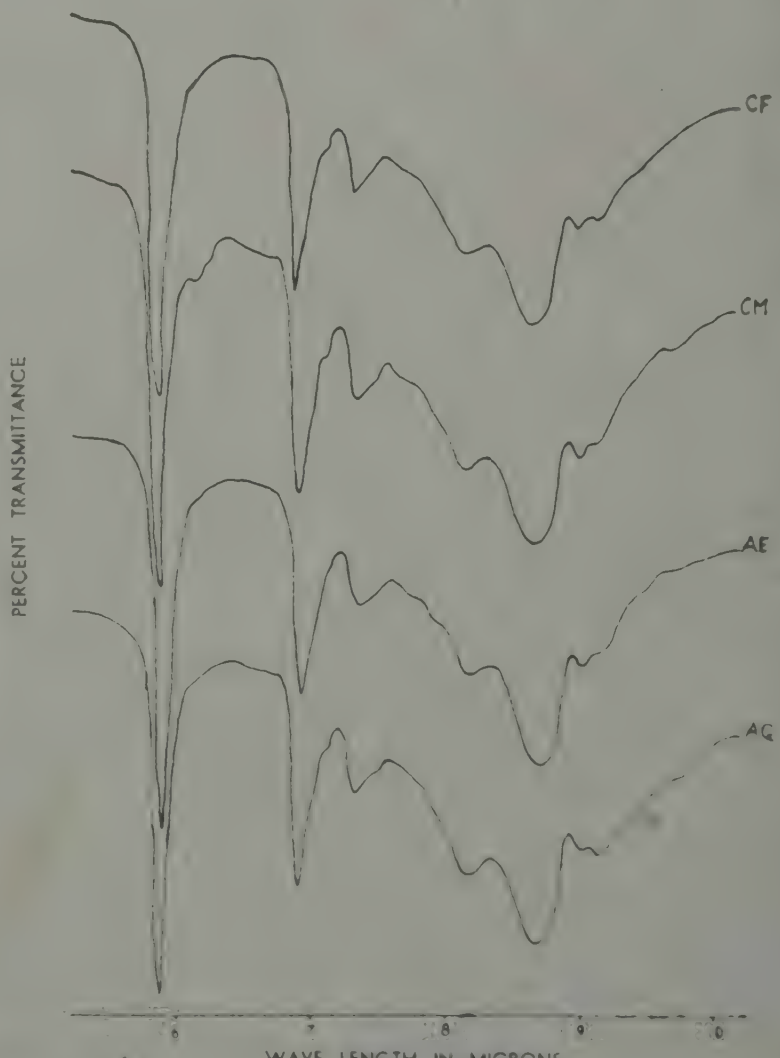

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Fig. 1. Absorption spectra of four different aqueous extracts of *C. molestus*. Fig. 2. Spectra of aqueous extracts of different mosquito species. Fig. 3. Absorption spectra of aqueous extracts of 9-day old mosquitoes. Fig. 4. Infrared curves from carbon disulfide extracts of four mosquito species. CM, *C. molestus*; AE, *A. aegypti*; AP, *A. pseudoscutellaris*; AQ, *A. quadrimaculatus*; CF, *C. fatigans* and CF (wild), *C. fatigans*.

fatigans (W) are practically identical. Infrared absorption curves obtained from extracts of male specimens revealed no differences between the sexes of any species.

In order to determine if any spectral changes occur between the newly-emerged adults and the more mature specimens, extracts (aqueous) were prepared from mosquitoes at seven and fourteen days of age. The most marked differences between these and the 24-hour old adults is seen by comparing Fig. 2 and 3. Extracts of the older specimens show a tall peak at 6.8μ and the disappearance of the peak at 7.0μ. Also, each extract represented in Fig. 3 shows deeper bands in the 8.6 to 10.6μ range and a change in shape of this broad band. Interspecific variation is exemplified by the comparatively deep band at 8.8μ which characterizes *C. fatigans* extracts.

Absorption curves from carbon disulfide extracts of different species are compared in Fig. 4. Although there appeared to be slight quantitative differences in the 7.6 to 10.0μ range, it was not possible to distinguish between them with any degree of certainty. Typical lipid bands are seen at 3.5, 5.85 and 6.95μ. This spectrum does not change appreciably with either the age or the sex of the mosquitoes.

GENERAL DISCUSSION

Judging from the mosquito species thus far studied, it is possible to differentiate between them on the basis of subtle, consistent differences in their infrared absorption spectra. Whether all species of mosquitoes could be characterized by individually distinct infrared patterns remains to be seen. When it is realized that basically the same absorption curves are obtained from viruses, bacteria and other biological material as for mosquitoes, it becomes obvious that biochemical differences between species of one kind of insect must necessarily be of small magnitude. Nevertheless, the reproducibility of nature is reflected by the uniformity of the absorption spectra which characterize a species at the molecular level.

Although infrared curves were obtained throughout the 2-16μ range, the most important part of the spectrum for purposes of differentiation lies between 6 and 11μ. Unfortunately, however, this region is likewise the most complex from the standpoint of identification of certain bands as particular chemical components of biological systems. For example, it has been shown that desoxyribonucleic acid (DNA) is partly responsible for the absorption at 9.4 and 9.8μ. It may be that the small band at 9.4μ in the aqueous extract curves and the suggestion of a second band at 9.8μ in *C. molestus* represent DNA. In this connection, it is of further interest that the various nucleic acid constituents such as cytosine, guanylic acid, uridine, adenylic acid and adenosine show absorption maxima in the 9-10μ range. It is in this particular region that aqueous extracts of mosquitoes exhibit the broadest, deep band.

The fact that the results of our earlier studies (Micks and Scrollini, 1954) on lipid extracts and those reported here do not appear to coincide is doubtless due to the difference in instruments used in the two investigations. It is noteworthy that the lipid content of the species studied remains constant for at least two weeks during which time marked changes occur in the absorption spectra obtained from aqueous extracts. It is possible that the 24-hour spectra represent largely those biological systems and materials carried-over from the pupa stage and that the 7-14 day curves (which are identical) indicate changes due to maturation processes. The latter spectra show less absorption at most wave lengths than the 24-hour curves except in the 8.4 to 10.6μ region where the absorbency has increased. Although the older specimens used in the preparation of aqueous extracts were allowed to feed on sugar water, control groups given distilled water only showed that the diet did not alter the characteristic curves. This point is further emphasized by the marked similarity between the infrared curves obtained from laboratory-reared *C. fatigans* and another strain of the species which completed its development in sewage.

REFERENCES

Benedict, A. A. M. Pollard, and F. B. Engley, Jr. 1954. Infrared absorption studies of virus preparations. *Texas Repts. Biol. and Med.* 12: 21–29.

Benedict, A. A. 1955. Group classification of virus preparations by infrared spectroscopy. *J. Bacteriol.* 69: 264–269.

Blout, E. R., and M. Fields. 1948. On the infrared spectra of nucleic acids and certain of their components. *Science* 107: 252.

Blout, E. R., and M. Fields. 1948. Absorption spectra. VII. The infrared spectra of some nucleic acids, nucleotides and nucleosides. *J. Biol. Chem.* 178: 335–343.

Frazer, R. D. B., and J. Chayen. 1952. The detection of nucleic acid in tissues by infrared microspectrometry. *J. Exptl. Cell Research* 3: 492–493.

Levine, S., H. J. R. Stevenson, L. A. Chambers, and B. A. Kenner. 1953. Infrared spectrophotometry of enteric bacteria. *J. Bacteriol.* 65: 10–15.

Micks, D. W., and A. A. Benedict. 1953. Infrared spectrophotometry as a means for identification of mosquitoes. *Proc. Soc. Exp. Biol. and Med.* 84: 12–14.

Micks, D. W., and F. Scrollini. 1954. An infrared spectrometric study of the *Culex pipiens* complex. *Riv. di Parassit.* 15: 161–165.

Noll, H., and H. Bloch. 1953. A toxic lipid component of the tubercle bacillus. ("Cord factor"). II. Occurrence in chloroform extracts of young and older bacterial cultures. *Am. Rev. Tuberc.* 67: 16–40.

Randall, H. M., R. G. Fowler, N. Fuson, and J. R. Dangl. 1949. Infrared determination of organic structures. *D. Van Nostrand Co., Inc.*, New York, N. Y.

Smith, D. W., W. K. Harrell, and H. M. Randall. 1954. Correlation of biological properties of strains of *Mycobacterium* with their infrared spectrums. III. Differentiation of bovine and human varieties of *M. tuberculosis* by means of their infrared spectrums. *Am. Rev. Tuberc.* 69: 505–510.

Stevenson, H. J. R., and O. E. A. Bolduan. 1952. Infrared spectrophotometry as a means for identification of bacteria. *Science* 116: 111–113.

The Discriminant Function in Taxonomic Research

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ABSTRACT

The present trend in taxonomy is to recognize that there is a certain amount of variation in many morphological characters useful in insect identification. More measurements are being used largely because better equipment is available for making such measurements. Large numbers of measurements require some condensing process that will furnish one or more values to adequately describe the large assemblage. The mean and the variance are examples of such descriptive numbers.

There are other more complex statistical techniques that will, under certain circumstances, be of great help to the taxonomist. Many species may be divided into subspecies, varieties, or races for ecological reasons. Yet, if sufficient intergradation of the available morphological characters exists, a division of the species on the basis of one or two characters will be difficult. The discriminant function and allied methods in classification have been successfully used by anthropologists to classify bones according to sex. The same techniques may be used by the insect taxonomist to help him make the best decision possible as to the grouping of his material.

The use of discriminant functions to test the validity of five subspecies of Culicoides variipennis *(Coq.) is illustrated. Of the five subspecies three were well defined, one was indistinguishable from one of the three, and the fifth was intermediate. The technique for computing the discriminant functions is explained.*

The taxonomist faced with the problem of separating a close-knit taxonomic complex must make many perplexing decisions. Usually one or two characters will not be sufficient to separate all the taxa present. A large number of characters must be examined, and those chosen which will best discriminate between the taxa thought to be present.

Of course, the decisions are usually made without the help of statistical methodology; consequently, the taxonomist often has no means of checking their accuracy except by general principles, experience, and intuition. The object of this paper is to illustrate the application of a subjective statistical technique, the generalized discriminant function, to a subspecific study of the *Culicoides variipennis* complex. The particular characters used were chosen by the taxonomists by methods other than statistical.

The following quantitative characters were found by the taxonomists to have potential value when used with certain qualitative characters in separating geographical populations of the *variipennis* complex:

X_1, palpal ratio, length of segment III to its width.

X_2, length of wing, in millimeters, from the basal arculus to the wing tip.

X_3, number of antennal segments of the series IV-V-VI-VII bearing sensoria.

X_4, number of teeth at the apex of the mandible.

The first set of measurements was taken from a series of 23 specimens each from six presumed subspecies. In order to complete the series for several subspecies it was necessary to include specimens from scattered localities which as a result of the calculations were found to represent areas of intergradation. The results of these first calculations were poor, with excessive variation indicated for every subspecies but *variipennis*.

As a result of the first analysis we concluded that (1) measurements for analysis should be taken from a more or less "typical series" restricted to one locality or population and (2) the localities could be regrouped to represent five more homogeneous subspecies. Since the pooled within dispersion matrix will be required, an equal number of specimens in each subspecies will not be necessary, thus obviating the need of equal numbers in each subspecies. The means and 95% confidence limits of the "typical series" so chosen are presented in Table I.

TABLE I. Means and 95% Confidence Limits for Five Subspecies of the *Culicoides Variipennis* Complex.

Subspecies	Palpal Ratio (X_1)		Wing Length (X_2)		Mandible Teeth (X_3)		Extra Sensoria (X_4)	
	Mean	95% limits	Mean	95% limits	Mean	95% limits	Mean	95% limits
variipennis	3.06	2.52–3.60	1.76	1.53–1.99	14.44	12.11–16.77	0.11	0 –0.90
australis	2.53	2.19–2.87	1.54	1.39–1.69	11.93	9.86–14.00	2.75	0.93–4.57
sonorensis	2.23	1.99–2.47	1.26	1.16–1.36	12.17	9.94–14.40	0.83	0 –2.01
albertensis	2.40	2.13–2.67	1.60	1.39–1.81	12.22	10.96–15.90	0.65	0 –1.79
occidentalis	2.26	1.89–2.63	1.63	1.60–1.66	14.00	12.10–15.90	0.65	0 –1.79

Since five subspecies are involved, five discriminant equations were computed, as described by Rao (1952, p. 316).

L_1 (*variipennis*) $= 83.1\ X_1 + 229.5\ X_2 + 12.2\ X_3 - 1.6\ X_4 - 417.6$
L_2 (*australis*) $= 68.3\ X_1 + 197.5\ X_2 + 10.6\ X_3 + 3.1\ X_4 - 305.3$
L_3 (*sonorensis*) $= 60.1\ X_1 + 162.0\ X_2 + 10.5\ X_3 + 0.2\ X_4 - 232.7$
L_4 (*albertensis*) $= 65.3\ X_1 + 206.6\ X_2 + 10.4\ X_3 + 1.4\ X_4 - 308.9$
L_5 (*occidentalis*) $= 61.2\ X_1 + 209.9\ X_2 + 12.0\ X_3 - 0.4\ X_4 - 324.3$

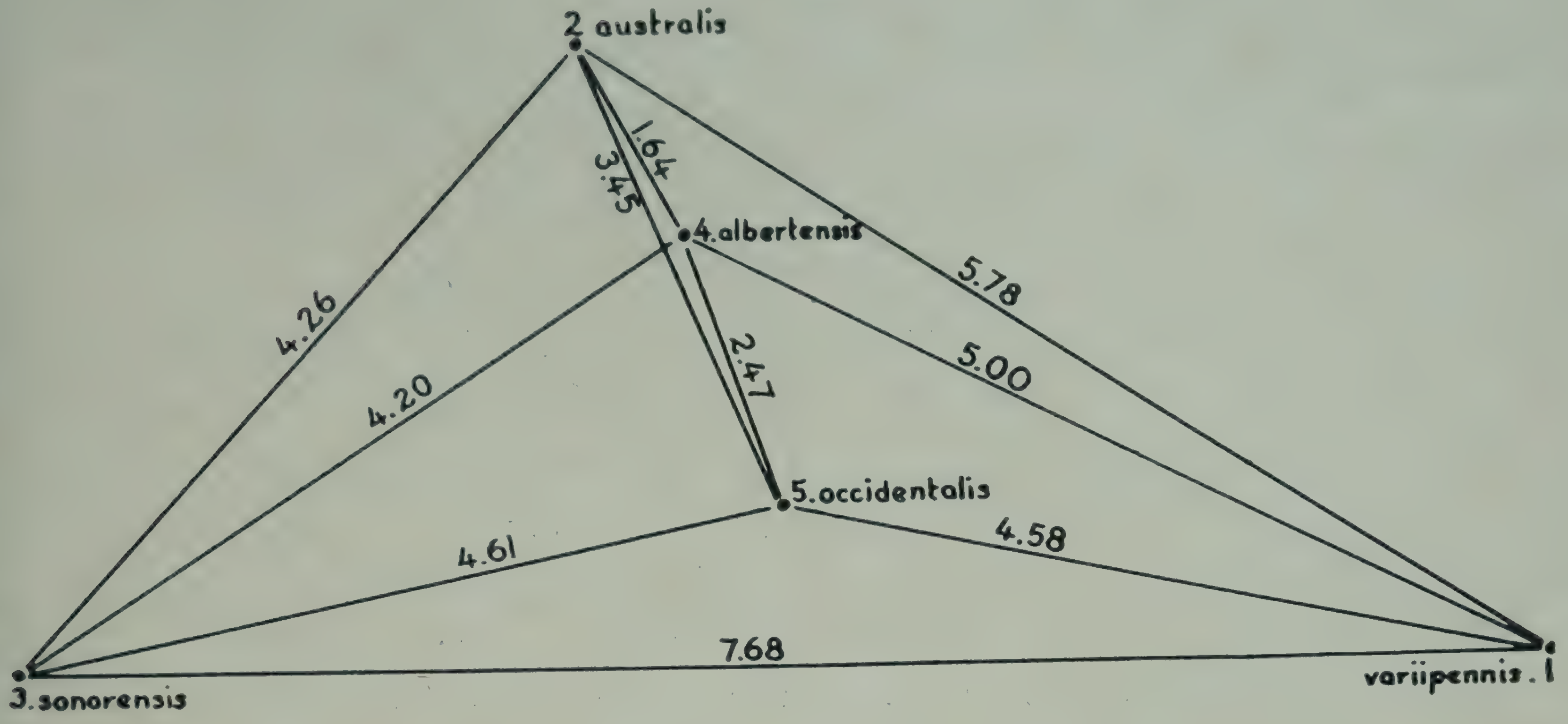
The maximum-likelihood method leads to the rule of assigning an individual whose measurements have been substituted in the L_r equations to that group for which L is the highest.

An indication of the power of discrimination inherent in the L_r equations may be obtained from Table II. The specimens in each "typical series" have been allotted to the five subspecies by the discriminant functions. It may be concluded that there are three fairly distinct populations which can be separated on the basis of the four measurements used in the analysis. The final separation of *australis* from *albertensis* must be made on the character of the male aedeagus, which is bare in *australis* and spinose in *albertensis*.

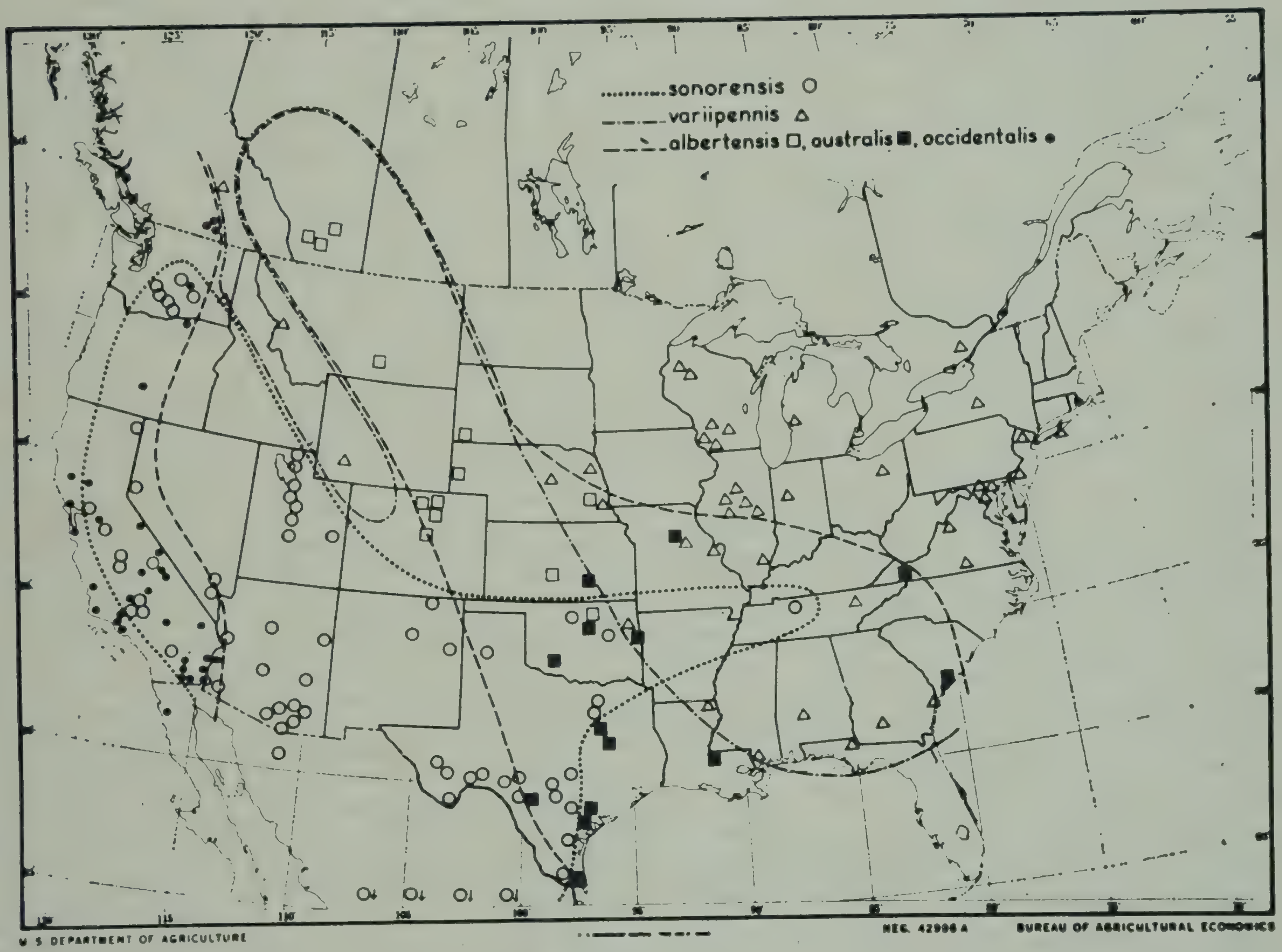
TABLE II. Percentage of the Specimens in each "Typical Series" Allocated to each Subspecies by the Discriminant Functions.

Subspecies	Number of specimens	Percent falling into—			
		variipennis	*australis-albertensis*	*sonorensis*	*occidentalis*
variipennis	36	97.2	0	0	2.8
australis	28	0	100.0	0	0
sonorensis	29	0	0	100.0	0
albertensis	27	3.7	89.9	0	7.4
occidentalis	20	0	20.0	0	80.0

A visual representation of the relationships among the species is provided by the distance between groups. All possible distances were calculated and the distance diagram, as shown in Fig. 1, constructed.


2 australis
4. albertensis
5. occidentalis
3. sonorensis
variipennis . 1
1.64
3.45
4.26
4.20
5.78
5.00
2.47
4.61
4.58
7.68

①


.... sonorensis ○
_ . _ . _ variipennis △
_ _ ` _ albertensis □, australis ■, occidentalis ●
U. S. DEPARTMENT OF AGRICULTURE
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BUREAU OF AGRICULTURAL ECONOMICS

②

Fig. 1. Distance diagram for five subspecies of *Culicoides variipennis* (Coq.) based on the Mahalanobis D^2 statistic.

Fig. 2. Geographical distribution of five subspecies of *Culicoides variipennis* (Coq.).

The success of the re-evaluation of the "typical localities" and the re-selection of the "typical series" is indicated by the results shown in Table II and Figure 1. A further use of the discriminant function would be to test populations of flies from localities where intergradation is known or suspected. This was done for 21 populations involving 163 specimens of all five subspecies. The results are given in Table III.

Generally, whenever there is a sufficient number of specimens, the tested populations fall within the subspecies to which the taxonomists allocated them. The few exceptions that cannot be allocated on the basis of the four morphological characters may then be placed a little more accurately by assuming that the subspecies exists in a genetically pure

TABLE III. Subspecies Allocation of Specimens of the *variipennis* Complex from 21 Localities, Including those with Intergradation.

Subspecies	Locality	Number studied	Percent falling into—			
			variipennis	*australis-albertensis*	*sonorensis*	*occidentalis*
variipennis	Hustberg, Tenn.	10	60	30	10	0
	Ellerville, Okla.	5	60	40	0	0
	Kilbourne, La.	3	100	0	0	0
australis	Stillwater, Okla.	12	0	92	0	8
	Petersburg, Mo.	11	18	73	0	9*
	Saltville, Va.	5	20	80	0	0
	Aransas, Tex.	10	0	90	0	10*
albertensis	Fort Collins, Colo.	9	0	89	0	11*
	Oral, S. Dak.	3	0	67	33	0
	Stafford Co., Kans.	4	0	75	0	25*
sonorensis	Camp Stanley, Tex.	4	0	50	25	25*
	Kerrville, Tex.	11	0	45	55	0
	St. David, Ariz.	3	0	0	100	0
	Wellton, Ariz.	6	0	0	100	0
	Moxee, Wash.**	13	0	38*	8	54
	Wiley, Wash.**	10	0	80*	0	20
occidentalis	Blythe, Calif.**	5	0	0	100	0
	Hueneme, Calif.	3	0	0	0	100
	Kamloops, B.C.	6	0	17*	0	83
	Orcutt, Calif.	9	0	89*	11	0
	Saratoga Springs, Calif.**	21	0	14*	86	0

*Probably erroneous, and can be corrected by using probability contours from distribution map.

**Assignment of specimens rests primarily on character of male aedeagus; possibly these represent undescribed populations.

state at the "typical locality" and covers an area determined by its ecological needs. As a rule the further one proceeds away from the center of distribution, the greater will be the probability that a given sample will include elements of intergradation from other subspecies whose ranges overlap that of the particular subspecies under study.

By use of the boundary of the range of each subspecies as defined in Fig. 2 by the taxonomists, contour lines may be drawn on a distribution map showing the areas within which each subspecies may be expected to occur according to 0.74, 0.18, 0.06, and 0.02 limits of probability. With such a map, the accuracy of which of course is limited by the sampling errors of the collections themselves and which is otherwise arbitrary, it is possible to re-allocate specimens assigned to subspecies from localities far removed from their center of distribution. This is especially valuable in the case of closely related subspecies with nonoverlapping distributions, such as *occidentalis* and *australis-albertensis*, in which a considerable number of specimens are found to overlap in all four characters simultaneously.

By use of probability gradients as discussed above it is possible to reassign a specimen from Moxee, Washington, which has the following L_r values:

L_1 = *variipennis* = 245.97
L_2 = *australis* = 268.84
L_3 = *sonorensis* = 267.47
L_4 = *albertensis* = 265.70
L_5 = *occidentalis* = 265.96,

which indicates, by our rules, that the specimen from which the measurements were taken should be allocated to *australis*.

If, instead of L_r, the quantity $L_r - \ln P$ is used, where P is the probability given by the contours, the following results are obtained:

L_1 = *variipennis* = 242.06
L_2 = *australis* = 264.93
L_3 = *sonorensis* = 264.66
L_4 = *albertensis* = 261.79
L_5 = *occidentalis* = 265.66,

which places the specimen in *occidentalis*. The breakdown for Moxee, Washington, on this basis is thereby:

Number of specimens	*variipennis*	*australis-albertensis*	*sonorensis*	*occidentalis*
13	0	8	15	77

instead of that shown in Table III. The correction probabilities, based on map contours would be 0.74 for *occidentalis*, 0.06 for *sonorensis*, and 0.02 for all other subspecies. Anything outside the last contour could have been eliminated by letting P = O for that area. Such a procedure would be too arbitrary, however, since the present boundaries are based only on the limited material examined thus far.

Perhaps the greatest value of running all available series through an analysis such as that shown in Table III would be to point out the possible existence of additional subspecies or lesser populations, which obviously are misfits in the present classification and have been arbitrarily assigned on male characters to positions at variance with the female characters. Examples in point are the series from Moxee and Wiley, Washington, and Blythe and Saratoga Springs, California.

THEORY AND WORKED EXAMPLE

A discriminant function is a linear function in several variables which will reduce the multiple measurements to a single variable. Symbolically the equations may be written:

$$L_r = \Sigma\,(\Sigma\,\lambda^{ij}\,\mu_{ir})\,X_j - 1/2\,\sum_i \sum_j \lambda^{ij}\,\mu_{ir}\,\mu_{jr} \quad i;\, j = 1, 2, 3, 4 \quad r = 1, 2, 3, 4, 5$$

$$= 1_{ir}\,X_{ir} + 1_{2r}X_2 + 1_{3r}X_3 + 1_{4r}X_4 - 1/2\,(1_{ir}m_{ir} + 1_{2r}m_{2r} + 1_{3r}m_{3r} + 1_{4r}m_{4r})$$

where $1_{ir} = \lambda^{i1}m_{ir} + \lambda^{i2}m_{2r} + \lambda^{i3}m_{3r} + \lambda^{i4}m_{4r}$

In order to evaluate these equations the within dispersion matrix is required. This is obtained as follows:

(1) For each subspecies there are *n* sets of four observations that furnish the needed data for computing the matrix of sums of squares and cross products corrected for the means.

$$\begin{pmatrix} \Sigma X_{i1}^2 & \Sigma X_{i1}X_{i2} & \Sigma X_{i1}X_{i3} & \Sigma X_{i1}X_{i4} \\ \Sigma X_{i1}X_{i2} & \Sigma X_{i2}^2 & \Sigma X_{i2}X_{i3} & \Sigma X_{i2}X_{i4} \\ \Sigma X_{i1}X_{i3} & \Sigma X_{i2}X_{i3} & \Sigma X_{i3}^2 & \Sigma X_{i3}X_{i4} \\ \Sigma X_{i1}X_{i4} & \Sigma X_{i2}X_{i4} & \Sigma X_{i3}X_{i4} & \Sigma X_{i4}^2 \end{pmatrix}$$

$$\text{where } \sum_{i=1}^{n} X_{i1}^2 = \sum_{i=1}^{n} (X_{i1} - \overline{X}_1)^2$$

In the present case the needed sums are:

Matrix elements	*variipennis*	*australis*	*sonorensis*	*albertensis*	*occidentalis*	Sum
X_1^2	2.67	0.82	0.41	0.49	0.67	5.06
X_1X_2	0.08	−0.16	0.00	0.05	−0.06	−0.09
X_2^2	0.47	0.16	0.07	0.31	0.04	1.05
X_1X_3	0.97	0.06	0.13	−0.02	0.00	1.14
X_2X_3	0.08	0.17	0.12	0.28	−0.20	0.45
X_3^2	48.49	29.86	36.14	10.67	18.00	143.16
X_1X_4	−0.33	−0.60	−0.43	1.52	0.48	0.64
X_2X_4	0.45	0.55	−0.02	−0.48	0.01	0.51
X_3X_4	−4.77	2.50	0.86	−0.67	0.00	2.08
X_4^2	5.5	23.25	10.14	34.67	6.55	80.17
Degrees of freedom	35	27	28	26	19	135

(2) The needed within-dispersion matrix is obtained by adding the individual matrices term by term and then dividing by the degrees of freedom. The degrees of freedom are $\sum_{r=1}^{5} (n_r - 1)$. The within-dispersion matrix, with 135 degrees of freedom, was calculated to be

$$\lambda_{ij} = \begin{pmatrix} 0.037\ 481 & -0.000\ 667 & 0.004\ 741 & 0.008\ 444 \\ 0.000\ 667 & 0.007\ 778 & 0.003\ 778 & 0.003\ 333 \\ 0.004\ 711 & 0.003\ 778 & 0.593\ 852 & -0.015\ 407 \\ 0.008\ 441 & 0.003\ 333 & -0.015\ 407 & 1.060\ 447 \end{pmatrix}$$

(3) The inversion of λ_{ij} cannot be described here in detail for lack of space. The reader is referred to any good text on matrices, preferably C. Radhakrishna Rao's "Advanced statistical methods in biometric research", 1952, John Wiley and Sons, New York.

$$\lambda^{ij} = \begin{pmatrix} 26.804\ 937 & 2.509\ 455 & -0.224\ 725 & -0.235\ 790 \\ 2.509\ 455 & 129.388\ 260 & -0.439\ 034 & -0.854\ 496 \\ -0.224\ 752 & -0.439\ 035 & 0.946\ 594 & 0.029\ 145 \\ -0\ 235\ 790 & -0.854\ 497 & 0.029\ 145 & 1.691\ 999 \end{pmatrix}$$

where

$$\lambda^{ij} = \begin{pmatrix} \lambda^{11} & \lambda^{12} & \lambda^{13} & \lambda^{14} \\ \lambda^{21} & \lambda^{22} & \lambda^{23} & \lambda^{24} \\ \lambda^{31} & \lambda^{32} & \lambda^{33} & \lambda^{34} \\ \lambda^{41} & \lambda^{42} & \lambda^{43} & \lambda^{44} \end{pmatrix}$$

(4) The last set of values needed is the mean values of each character for each subspecies.

	X_1	X_2	X_3	X_4
variipennis	3.0583	1.7639	14.4444	0.1111
australis	2.5286	1.5357	11.9286	2.7500
sonorensis	2.2345	1.2552	12.1724	0.8276
albertensis	2.4037	1.6037	12.2222	1.7778
occidentalis	2.2550	1.6300	14.0000	0.6500

(5) The equations for L_r as given at the beginning of this section may now be evaluated. The equation for the subspecies *variipennis* (r = 1) is:

$$l_{11} = (26.804)\ (3.058) + (2.509)\ (1.734) + (-0.225)\ (14.444) + (-0.236)\ (0.111) = 83.132$$

$$l_{21} = (2.509)\ (3.058) + (129.388)\ (1.734) + (-0.439)\ (14.444) + (-0.854)\ (0.111) = 229.466$$

$$l_{31} = (-0.225)\ (3.058) + (-0.439)\ (1.734) + (0.947)\ (14.444) + (0.029)\ (0.111) = 12.214$$

$$l_{41} = (-0.236)\ (3.058) + (-0.854)\ (1.734) + (0.029)\ (14.444) + (1.692)\ (0.111) = -1.619$$

$$\text{constant} = -1/2\ [(83.132)\ (3.058) + (229.466)\ (1.734) + (12.214)\ (14.444) + (-1.619)\ (0.111)\ ] = -417.624$$

$$L_1 = 83.132\ X_1 + 229.466\ X_2 + 12.214\ X_3 - 1.619\ X_4 - 417.624$$

The calculation of the distances from which figure 1 was drawn involves quantities derived from the tables used in the inversion of the within-dispersion matrix. The first step consists in making a completely uncorrelated set out of the means given in part (4). The process is easy, but the reader is again referred to Rao, pages 293–4, for a detailed explanation. In the present case the uncorrelated set of means was calculated to be:

	X_1	X_2	X_3	X_4
variipennis	15.7970	20.6334	13.3757	−1.2450
australis	13.0609	17.9369	11.0109	2.3772
sonorensis	11.5418	14.6946	11.4505	0.1196
albertensis	12.4158	18.6834	11.3112	1.0971
occidentalis	11.6477	18.9518	13.1599	−0.3204

The distance of one subspecies from another is the square root of the sum of the squared differences of each character for the two subspecies chosen. For example:

$$D^2\,[(1)\ \textit{variipennis} - (2)\ \textit{australis})] = [(15.7970-13.0609)^2 + (20.6334-17.9369)^2 + (13.3757-11.0109)^2 + (-1.2450-2.3772)^2] = 33.4870$$

$$D = \sqrt{33.4870} = 5.7868$$

DISCUSSION

R. R. Sokal. A limitation of the discriminant function as a systematic tool is that it requires an a priori separation of the individuals into recognizable categories, perhaps on the basis of cytological or some other such evidence. This is occasionally possible, but is not typically so in systematic problems. Usually we must find a way of grouping the material first.

J. U. McGuire, Jr. Dr. Sokal is correct. A known population is needed for good discrimination. However, the method may be used to determine if the chosen populations are "good" or not, which was done in the case I have described.

O. W. Richards. Is it not important to have a method of choosing what characters to measure?

J. U. McGuire, Jr. Yes, it is.

R. R. Sokal. Regarding Dr. Richards' question, the original description of the discriminant function assumes that one studies only characters that differ in their means for the populations studied. These characters therefore have overlapping frequency distributions that differ in their means. Because of this, useless characters can be eliminated at the start.

H. Townes. Dr. McGuire's case seems to be one of the kind that Dr. W. L. Brown is interested in; namely, there are a number of clines going in various directions, and the characters chosen by the taxonomist to distinguish subspecies do not always group together the individuals making the most coherent populations.

J. U. McGuire, Jr. I agree, although I understand that the initial premises are slightly different.

H. Townes. I believe that these mathematical computations illustrate the way that taxonomists work. Although they do not put down their data and conclusions in statistical terms, they actually base their conclusions on statistical correlations, working toward a maximum correlation of the characters that they find.

J. U. McGuire, Jr. I agree. The amount of actual evaluating and re-evaluating of the different characters finally used is tremendous. In our particular case, Dr. Wirth constructed hundreds of frequency distributions before making his final choice of the characters to be used.

Hemolymph Proteins and Their Use in Taxonomic Studies[1]

By W. P. Stephen
Oregon State College
Corvallis, Oreg.

ABSTRACT

A study of the hemolymph proteins of seven species of insects was undertaken to determine the inter- and intra-group relationships as expressed by the fractions. The banding was compared to that of human and bovine sera, and the mobility of the fractions was plotted in millimeters of migration from the point of application.

Using samples that ranged from 0.0005 to 0.005 ml., the species studied yielded from two to four proteins, excluding the fraction at the point of application. One fraction with a mobility of 8 to 10 millimeters was found to be common to all except one species. The two species of roach, P. americana *and* B. orientalis, *had the most nearly identical patterns on qualitative and quantitative analysis. The other species showed considerable difference in protein fractions.*

There was no indication of any fraction in all of the species which even remotely resembled the albumin from human serum. Several of the species exhibited fractions that corresponded in mobility to alpha, beta and gamma globulins of human serum.

INTRODUCTION

With the development of micro-analytical instruments for the quantitative and qualitative evaluation of proteins, there has been a marked increase in investigations of the tissue and body fluids of organisms which previously were considered too minute for accurate study. The continual refinement of techniques associated with micro-electrophoresis has made it possible to analyze the hemolymph of individual insects, and, in many cases, permits numerous replications from a single specimen.

Little comparative information is available on the protein composition of insect hemolymph or tissue. There is, however, a wealth of information on mammalian forms, particularly man, and this suggests that marked quantitative differences exist in various pathological states. Perhaps the most significant point is that the protein blood fractions in non-pathological humans are all similar, yet comparisons of electrophoretic patterns from different individuals reveal subtle, constant, characteristic differences, permitting the separation of one individual from others (Bernfeld, Donahue, and Homburger, 1953). Additional information from an electrophoretic study of the blood serum of several small animals is significant in the light of this study. Gleason and Friedberg (1953) found that, while five or six peaks are common to the pattern of human blood, analyzed sera of the turtle, mud puppy, frog, and salamander exhibited 7, 7, 10, and 3 components, respectively. Rats, mice, and opossums yielded the same protein fractions found in man, however, with marked quantitative differences, while the poikilotherm differences were distinctly qualitative.

Further verification of the specificity of electrophoretic patterns revealed that the serum of the turtle, snake, bullfrog, horseshoe crab, and snail produced constant reproducible patterns for each species under investigation (Deutsch and McShan, 1949). Dessauer and Fox (1956) have erected a tentative ordinal key to the Amphibia and Reptilia based on the plasma proteins.

Several papers dealing with the protein determination of insect hemolymph are briefly outlined by Clark and Ball (1956) who, in turn, report on the electrophoretic patterns of three species of lepidopterous larvae, two species of culicine mosquitoes, and the roach *Periplaneta americana* (L.). Extrapolation from these studies tends to indicate that comparative protein analysis not only distinguishes large categories in a qualitative manner, but could be used to differentiate between populations (and individuals) of polytypic forms.

METHODS

Several types of electrophoretic apparatuses were tested prior to the initiation of these studies and of these the Durrum type hanging strip cell, as manufactured by Spinco Division of Beckman Instruments, was selected. Selection of a specific apparatus was based

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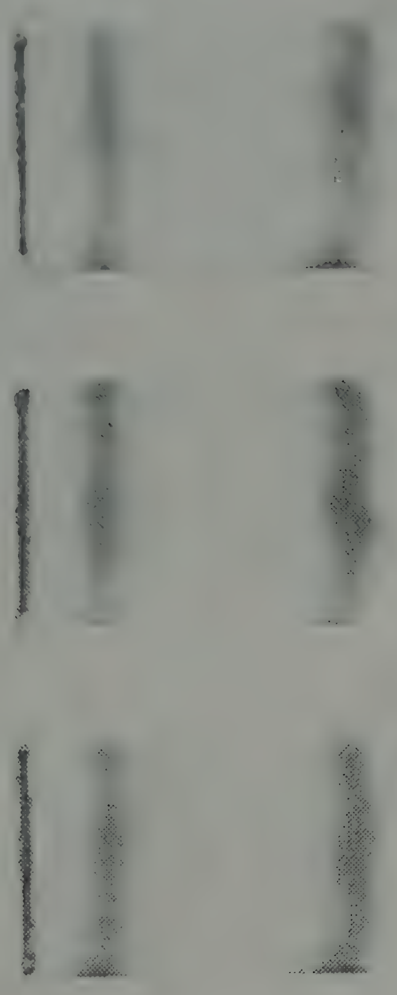
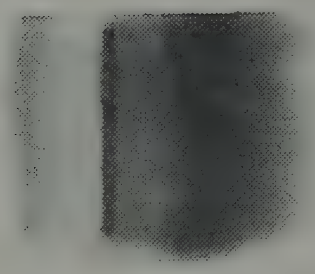
[1] Aided by a grant from the Graduate School Research Fund, Oregon State College and Technical Paper No. 1014, Oregon Agricultural Experiment Station.



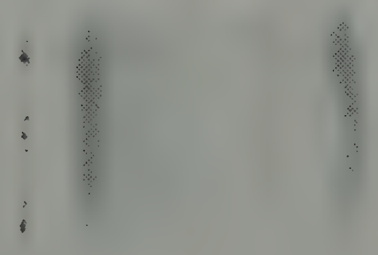
Periplaneta americana

Phormia regina

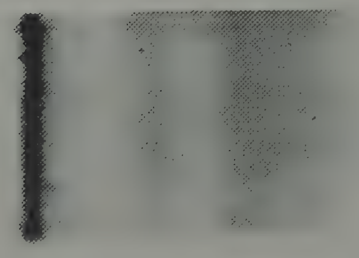
Smerinthus cerisyi



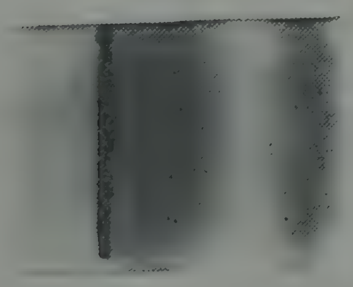
Pleocoma minor



Blatta orientalis



Lichnanthe rathvoni



Oncopeltus fasciatus

Human

primarily on reproducibility, absence of protein fraction trailing, and distinctness of fraction bands (Fig. 1). The methods used with this apparatus in the analysis of human serum proved to be most satisfactory for the insect hemolymph run.

Whole samples of insect "blood" were obtained by making a direct heart puncture on the insect as close to the base of the abdomen as possible. A calibrated micropipette was inserted and the desired quantity of blood was transferred immediately to the equilibrated buffer-saturated strips in the cell. Standard methods were employed throughout the series of studies, using a veronal buffer with a pH of 8.6 and with an ionic strength of 0.05. The strips were moistened with buffer and placed in the cell where they were allowed to equilibrate at the operating current for at least an hour prior to sample application. The samples were run at a current of 15 ma. for a period of six hours, dried, and stained in bromphenol blue for six hours. Following two rinses in 5% acetic acid and fixing in a mixture of 5% acetic acid and 3% sodium acetate, the strips were dried and set aside for at least two days to permit color oxidation. The strips were scanned, using the Spinco Analytrol. In a long series of tests using time and current variables, it was found that running the samples at a current of 15 ma. for a period of six hours resulted in the least protein trailing and much more compact bands.

Seven insect species were used in these trials: the roaches *Periplaneta americana* (L.) and *Blatta orientalis* L.; the large milkweed bug, *Oncopeltus fasciatus* (Dall.); the black blow fly, *Phormia regina* (Meig.); the willow sphingid, *Smerinthus cerisyi* Kby.; and the scarabs, *Pleocoma minor* Linsley and *Lichnanthe rathvoni* (Lec.) Only the female adults of the above species were used, as distinctive protein differences exist between the sexes and between the adults and immature forms. This will be reported upon in detail in a subsequent paper.

The quantity of hemolymph used varied from 0.005 to 0.01 ml., depending upon the protein concentration. In those species in which the protein concentration was extremely high, it was necessary to reduce the size of the sample to obtain accurate comparative data using the Analytrol scanner, and to reduce the amount of fraction trailing. In general, samples of 0.002 to 0.003 ml. proved to be most adequate, and such sample sizes were used as a standard except where otherwise indicated.

Samples of human sera were run and used as the comparative standard in determining or locating the specific hemolymph fractions found. The areas under the curves obtained from the scanned strips were calculated and presented as a percentage of the total protein. In all calculations the point of application was not included as a specific protein, nor was the stain intensity considered in the total protein concentration. This is undoubtedly undesirable, however, until the melanin can be quantitatively accounted for and subsequently removed as a source of error, the point of application is indicated only as source point 0 in Table 1. In the hemolymph of all species here studied, there appeared, to a greater or lesser degree, a distinct grey or black band immediately after the sample was applied. It is suspected that this fraction represents, in part, oxidized melanin, and in no case was it observed to move in the electric field. In addition to the melanin, however, there is an apparent band at the application point which moves negligibly and spreads perhaps one or two millimeters to either side of the origin. Although this acts similarly to fibrinogen, it has been shown that such a fraction does not precipitate over the phosphate concentration range at which fibrinogen in human plasma has been thrown down.

The various protein fractions are indicated on the basis of their mobility in millimeters in a given buffer at a given current. This is not meant to imply that only one protein appears at each given peak, but rather that the peak represents the proteins which have migrated at a similar speed. It should also be noted that the absence of a given fraction in a species sample may mean one of two things: either the fraction is absent, or else that it is present in such trace amounts that the method employed does not permit the investigator to identify it.

← Fig. 1. Strips stained with bromphenol blue showing the banding of proteins in seven insect species as compared with human blood. The three strips of *Periplaneta americana* represent samples from three different individuals and indicate accuracy in replication. The narrow dark bands are the points of application.

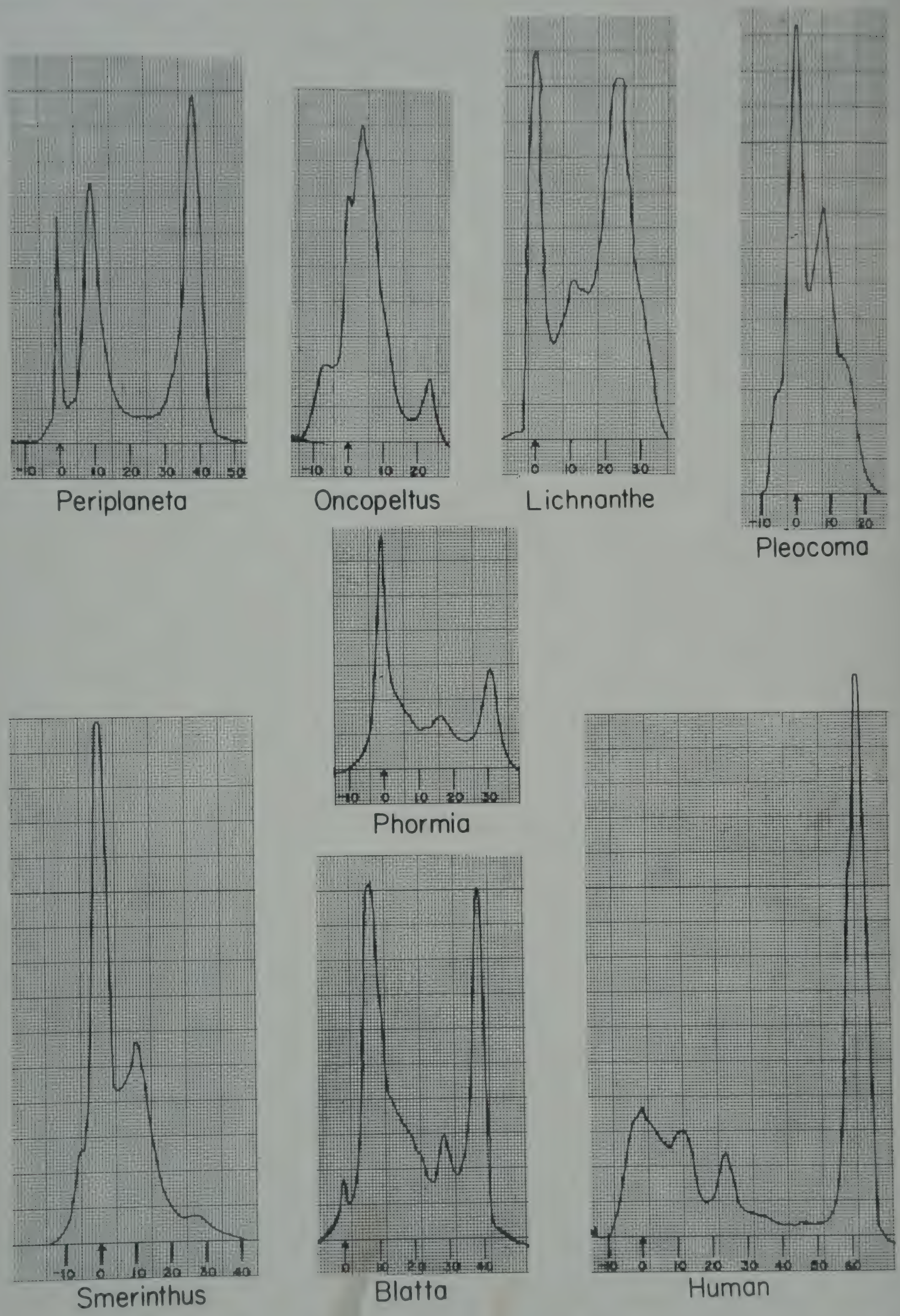


Fig. 2. Scan patterns of seven insect species and of human blood. The peaks represent the protein fractions in each species and the areas under the curves are used to calculate the percentage of total protein.

RESULTS

A study of the strips and the Analytrol scan indicates that there are from two to five principal proteins in the species studied. The count does not include the point of application as mentioned earlier. Contrary to the findings of Clark and Ball (1956), Drilhon (1954), Florkin and Duchâteau (1943), and Florkin and Gomez (1939), none of the fractions had a migration pattern that corresponds to the albumin of human or bovine serum. This finding corresponds to that of Wunderly and Gloor (1953) working on *Drosophila* larvae. The greatest mobility was exhibited by a fraction (s) common to both *P. americana* and *Blatta orientalis*. This peak was found from 34 to 38 millimeters from the origin and corresponds very closely to the mobility of alpha 1 globulin of human serum. The fractions with mobilities comparable to those of human fractions are indicated on Table I.

TABLE I. Distribution of Protein Fractions in Insect Hemolymph.

Source of sample	Migration of fraction from origin in millimeters								
	–8 to–3	1–2	8–10	12–15	18–20	23–25	28–30	34–38	63–68
P. americana (15)*			X					X	
B. orientalis (5)			X				X	X	
O. fasciatus (5)	X		X			X			
P. regina (3)			X		X		X		
S. cerisyi (2)	X		X				X		
P. minor (8)	X		X	X					
L. rathvoni (2)	X	X		X		X			
Human	————gamma————			beta		alpha 2		alpha 1	albumin

*The number in parentheses indicates the number of individuals sampled.

In a series of over sixty hemolymph samples from the American roach, *P. americana*, two main protein peaks can be observed (Table I, Figs. 1 & 2). This is contrary to the findings of Clark and Ball (1956) who recorded six fractions for this species. The size of the sample was varied from 0.003 to 0.05 ml., but patterns similar to those recorded by the above authors were not found. On the 0.05 ml. sample it was possible to note two weak negatively migrating bands, which were not recorded in their work. The concentration of protein, at the two major bands when samples greater than 0.005 ml. were used, was so great that fraction trailing obscured the area immediately about the peaks.

The samples from the oriental roach, *B. orientalis*, revealed three protein peaks, two identical with those of the American roach and a third just inside of the outer band (Table I, Figs. 1 & 2).

TABLE II. Percent of Total Protein Represented by Each Fraction.

Source of sample	–8 to–3	1–2	8–10	12–15	18–20	23–25	28–30	34–38
P. americana (5)*			68.5					31.5
			63.0					37.0
			66.7					33.3
			62.1					37.9
			52.5					47.5
B. orientalis (2)			58.5				12.5	29.0
			61.2				10.9	27.9
O. fasciatus (2)	12.7		77.5			9.8		
	10.0		80.0			10.0		
P. regina (2)			30.1		15.0		54.9	
			30.9		13.1		56.0	
S. cerisyi (2)	9.3		83.2				7.5	
	10.8		81.5				7.7	
P. minor (3)	7.4		75.3	17.3				
	5.9		76.3	17.8				
	5.7		78.2	16.1				
L. rathvoni (2)	1.6	11.9		20.6		65.9		
	1.5	13.9		21.6		63.0		

*The number in parentheses indicates the number of individuals sampled.

In all of the species except *Lichnanthe rathvoni*, the fraction with a mobility of 8 to 10 millimeters was found to be common and in most cases it was the protein of greatest concentration. Three different peaks were evident in all species with the exception of the American roach with two, and the scarab, *Lichnanthe rathvoni*, with four. Evidence of fractions with mobilities similar to the alpha and beta globulin fractions of human blood can be seen in Table I. The proteins that are listed in that table as having a negative mobility of −8 to −5, −3, and 1 to 2 may be included in the range of gamma globulin of human serum, for gamma globulin of human serum is not a single protein but rather a number of proteins with similar mobilities which can not be separated using available methods.

Table II offers quantitative data with the protein fractions expressed as the percentage of total protein using two to five different individuals within each species.

GENERAL DISCUSSION

With the meager data available it is impossible to draw conclusions on the systematic implications of hemolymph proteins. However, certain similarities can be pointed out at this stage. On the basis of the proteins, the American and the oriental roach appear to be the most closely related. Both species have a quantitative and qualitative similarity in two of the fractions. A third fraction is peculiar to the oriental roach but is present in trace amounts.

The apparent qualitative differences between the two scarabs is difficult to account for; however, further work on a number of species within this highly complex group may contribute to a better understanding of relationships within the family.

There is considerable quantitative variation in the protein among individuals of the same species, but a series of runs indicates that, if care is exhibited in selecting individuals of the same age and sex, these differences will not overlap the patterns obtained even from closely related species.

The technique is extremely sensitive as only 0.0005 to 0.005 ml. of hemolymph are required for optimum results. This small size of sample permits a direct electrophoretic analysis of the hemolymph of even the smaller insects without resorting to pooled blood samples or whole body homogenates.

REFERENCES

Bernfeld, P., V. M. Donahue, and F. Homburger. 1953. Characteristic individual electrophoretic patterns in humans. *Proc. Soc. Exper. Biol. and Med.* 83: 429–434.

Clark, E. W., and G. H. Ball. 1956. Preliminary microelectrophoretic studies of insect proteins. *Physiol. Zool.* 29: 206–212.

Dessauer, H. C., and W. Fox. 1956. Characteristic electrophoretic patterns of plasma proteins of orders of Amphibia and Reptilia. *Science* 124: 225–226.

Deutsch, H. F., and W. H. McShan. 1949. Biophysical studies of blood plasma proteins. *Jour. Biol. Chem.* 43: 1165–1172.

Drilhon, A. 1954. Étude électrophorétique des protéines de l'hémolymphe du *Bombyx mori* au cours de son cycle de croissance. *Compt. Rend. Acad. Sci.* 238: 2452–2454.

Florkin, M., and G. Duchâteau. 1943. Le graphique de précipitation par les phosphates du plasma sanguin d'un insecte (*Hydrophilus piceus*). *Acta. Biol. Belg.* 3: 1–2.

Florkin, M., and J. Gomez. 1939. Rapport albumines-globulines du plasma sanguin d'un insecte. *Assoc. Franç. Avance. Sci.* 63ᵉ sess., p. 684.

Gleason, T. L., and F. Friedberg. 1953. Filter-paper electrophoresis of serum proteins from small animals. *Physiol. Zool.* 26: 95–100.

Wunderly, C., and H. Gloor. 1953. Versuche zur Charakterisierung der larvalen Blutproteine normaler und letaler Genotypen von *Drosophila* mittels Papier-Elektrophorese. *Protoplasma* 42: 273–282.

Incident Light Photomicrography and Other Useful Techniques in the Study of Minute Insects

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ABSTRACT

The author briefly describes: (1) a technique for photographing minute (ca. 0.5–2.0mm. long), dark, opaque insects with a Leitz Ultropak Incidental Light Illuminator; (2) techniques of preparing and orienting specimens for photographing with Ultropak; (3) the Stereo Polarizer, which enables one to achieve stereoscopic vision in studying cleared, slide-mounted specimens with a binocular monobjective microscope.

The Ultropak may be attached, without ocular, directly to a photomicrographic camera. Use of high power Ultropak achromatic objectives (22X, 11X) provided with slip-in diaphragms gives a high degree of resolution and contrast, the needed depth of focus and flattening of the field, and greatly reduces the effect of axial spherical aberration.

The Stereo Polarizer allows each eye to receive only the image that is formed through its corresponding side of the objective.

Our knowledge of certain groups of minute insects has been limited by difficulties of technique. Frequently, these problems can be solved by adopting, directly or with modification, techniques or equipment that have been developed for other areas of investigation. Two such pieces of equipment — the Stereo Polarizer and the Leitz Ultropak Incident Light Illuminator — are briefly described herein[1] together with a short discussion of specific applications to some entomological problems.

The writer is indebted to: Mr. John R. Provan of the Scientific Instrument Division, Bausch and Lomb Optical Company, Chicago, for calling his attention to the usefulness of the Stereo Polarizer in the study of slide-mounted materials; to Mr. G. F. Hammond, Laboratory and Inspection, Products Sales Department, Bausch and Lomb Optical Company, Rochester, New York, who, at Mr. Provan's request, kindly supplied a detailed account of the principle of the Stereo Polarizer, including a diagram of the light paths, for publication purposes (the description given here is drawn largely from that account); and to Mr. W. H. Kessel of W. H. Kessel & Co., Scientific Instruments, Chicago, for introducing him to the use of Ultropak, for his kindness in furnishing accessories for experimental work, and for supplying a bibliography on the application of Ultropak to biological work.

INCIDENT LIGHT PHOTOMICROGRAPHY OF MINUTE INSECTS

Some entomologists are acquainted with the use of Ultropak for the examination of insects with incident light at high magnifications. Few, if any, seem to have been aware of the potential value of Ultropak for the photography of minute insects for illustrative purposes.[2] Many minute (ca. 0.5–2.0mm. long) dark, opaque forms, which are generally regarded as presenting some of the most difficult problems in photography with incidental light, can be satisfactorily photographed by using a Leitz Ultropak illuminator coupled to a photomicrographic camera.

The Ultropak illuminator is a device with coaxial optical and lighting systems wherein light is directed at the object, at a small angle from the optical axis, through ring condensers surrounding the objective. The light source is located in a lamp attachment at the side of the unit. The light is directed horizontally from the lamp through condensing lenses to an obliquely placed ring-shaped mirror surrounding the optical axis; the mirror reflects the light downward through the ring condensers, which bend and focus the light on the object. A holder for filters and adjustable sector diaphragms is situated between the lamp attachment and the lamp condenser. The light source is an 8-volt, 0.6-amp. filament bulb. Attachments with more intense light sources, including carbon arc, are available.

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[1] A more comprehensive, illustrated version of this paper will be published in, *Fieldiana, Zoology*, Vol. 39, probably in 1957.

[2] The only laboratory with which the writer is personally acquainted, where Ultropak is used for this type of photography, is the Bio-Graphic Unit of Science Service, Department of Agriculture, Ottawa, Canada. This organization apparently began using the equipment after the writer had called their attention (early in 1955) to its usefulness in photographing insects. Since then, an article by a member of their staff (Klosevych, 1956) was published in Bio-Graphic Quarterly and was available to members of the Congress at Montreal in 1956.

For the photography of specimens 0.5-1mm. long. the writer uses a 22X objective, with slip-in diaphragm, and for specimens 1.0-2.0mm. long, an 11X objective with diaphragm. The Ultropak is attached directly to a Bausch and Lomb Model H photomicrographic camera by means of a Society thread adapter. The use of an ocular, in photographing specimens of this size, is unnecessary. Indeed, if the illuminator is attached to a monobjective microscope that is coupled to the camera, the ocular should either be eliminated or be of very low magnification, for example, about 2X. Otherwise, in photographing a specimen of the size indicated, and with the objectives indicated, the resultant image will not only be too large for a 3¼ x 4¼ in. or even a 4 x 5 in. negative, but will have less resolution and depth of focus. If the image is scaled down to usable size through the use of a lower power objective and an ocular, the resolution is greatly reduced and a more intense light

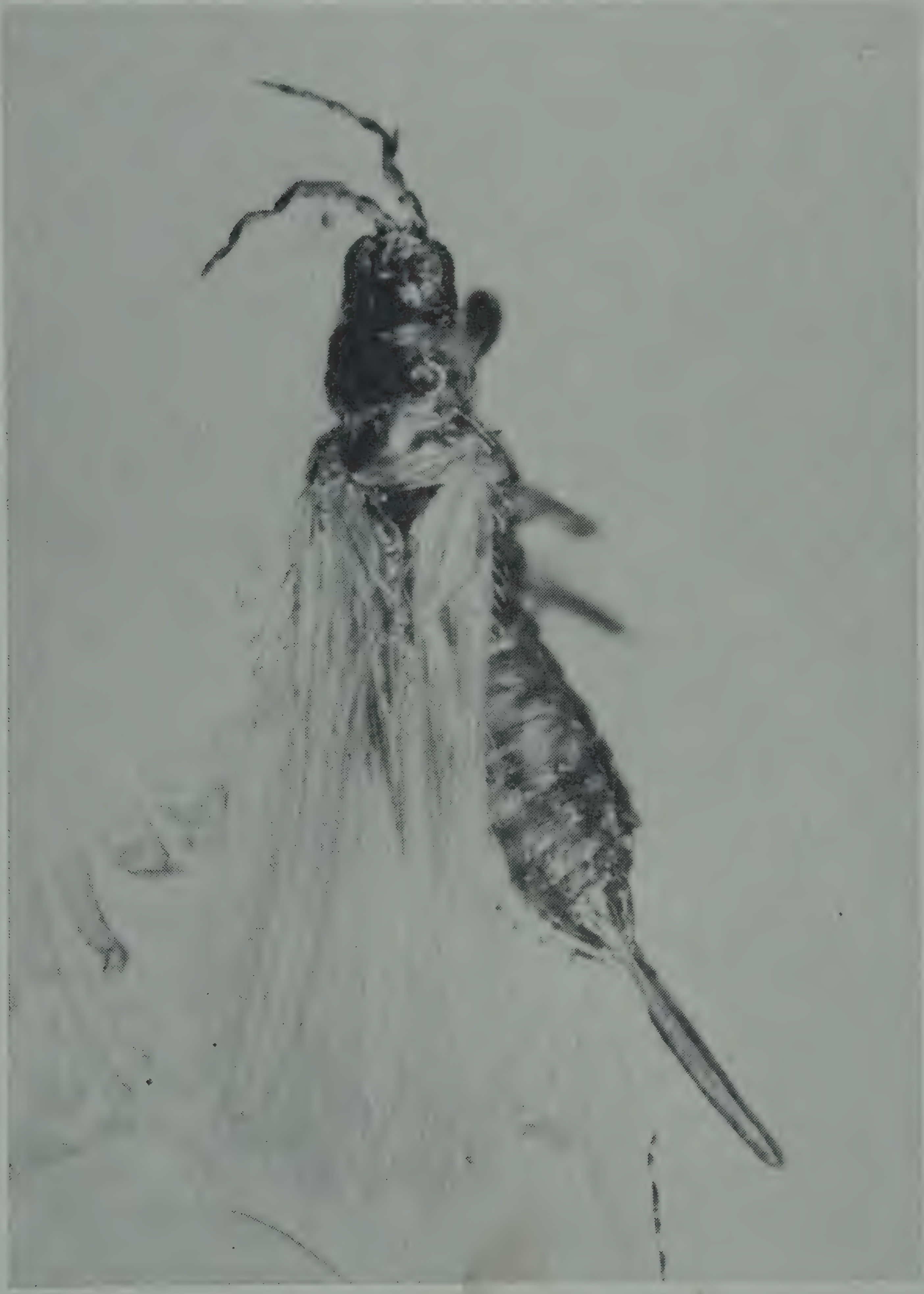

Fig. 1. *Stenurothrips bagnalli* Stannard X73. A thrips in Baltic amber. Photographed with Ultropak. Objective lens UO 11X; N.A. 0.25; aperture of slip-in diaphragm, 1.65 mm. Light source, 8 volt, 0.6-amp, filament bulb. Bellows extension, 300 mm. Film, Panatomic-X. Exposure, 5 seconds.

source is needed. For maximum resolution and contrast, it is desirable to use as high power an objective as possible, without ocular. Through the use of slip-in diaphragms, the field is greatly flattened and the noticeable effect of axial spherical aberration of the lens is greatly reduced. In testing objectives that were provided with the smallest diaphragms, the author was unable to detect any change in focus across the diameter of the field or any convergence of field toward the edge.

For photographic specimens 2.0–4.0mm. long, one may use lower power (5X and 6.3X) Ultropak objectives with diaphragm, and without ocular. However, in most such instances, unless special problems of illumination are involved, superior results would be obtained by using a 16 or 20mm. Micro Tessar, Micro Luminar, Micro Rattar, or a similar lens that is provided with an iris diaphragm.

Examples of photographs taken with Ultropak and of line drawings made from photographs taken with Ultropak may be seen in a recent paper by the author (Wenzel, 1955).

Obviously, specimens of such small size cannot be oriented manually in the photographic field without considerable difficulty. Specimens up to 1.25mm. in length may be glued to short pieces of human hair that are attached to truncated paper triangles (Wenzel, 1944, p. 53). The larger specimens are "pointed", that is, glued to fine-tipped standard American style "triangle" points. A pin ½ inch long is run through the base of the triangle and inserted into the receiving tip of a mechanical holder. The holder can be rotated through vertical and horizontal planes; changing the angle of the pin in the holder allows for rotation of the specimen in additional planes. The mechanical holder, in turn, is manipulated by a mechanical stage so as to provide forward-backward and lateral movement. Additional mechanical orientation of the specimen is possible if the mechanical stage is of the revolving type. The mechanical stage is mounted on a vertical focusing stage.

Before the specimens are glued to the "hair mounts" or triangles, they must be thoroughly degreased. A degreasing apparatus similar to that described by Southgate (1953, p. 10) is effective. Ethyl acetate is the degreasing agent. Dirty specimens may be cleaned by being soaked in a good laboratory glass cleaning detergent for 30 minutes, brushed in liquid with a very fine soft camel hair brush, rinsed and dried.

THE STEREO POLARIZER

Interpreting three-dimensional relationships of structures is often difficult when one studies cleared, slide-mounted specimens through a monobjective microscope, using transmitted light. Stereoscopic viewing of such specimens is most helpful and can be achieved through the use of a binocular monobjective microscope equipped with a Stereo Polarizer, if the specimen is thicker than the depth of focus of the objective used.

The components of the Bausch and Lomb Stereo Polarizer are: (1), a circular substage polarizer which consists of two semi-circular pieces of polaroid material, cemented together between two cover glasses in such a manner that their vibration planes are at right angles to each other; (2), two polaroid cap analyzers.

The sub-stage polarizer must be fitted beneath the condenser of the microscope. The cap analyzers are slipped over the eyepieces and so oriented that their vibration planes are parallel with the vibration planes of the corresponding half of the substage polarizer and at right angles to the planes of the opposite half. Each ocular now admits light only from the corresponding half of the objective, the right eye gets only the image formed through the right half of the objective and the left eye the image formed through the left half. The fused unlike images thus received cause the specimens to stand out in stereoscopic relief. The stereoscopic effect is most pronounced when the condenser is racked down.

Rotation of the analyzers through 90° causes the eyes to receive images formed through the opposite halves of the objective. In this way, a "pseudoscopic" effect is achieved. Since the object is transparent, the "pseudoscopic" effect gives one the impression of looking at the specimen from the reverse side.

REFERENCES

Heine, H. 1931. Der Ultropak. *Zeitschrift f. Wissenschaftliche Mikroskopie u. f. mikroskopische Technik* 48(4).

Klosevych, S. 1956. Photomicrography with incident light. *Bio-Graphic Quarterly* 2(3): 6–7, 2 Fig. (Science Service, Canada Department of Agriculture).

Southgate, B. J. 1953. A convenient method for degreasing insect specimens. *Entomologist* 86(1): 10.

Wenzel, Rupert L. 1944. On the classification of the histerid beetles. *Field Museum Nat. Hist., Zool. Series* 28(2): 51–151, 2 Fig., 9 Pl.

Wenzel, Rupert L. 1955. The histerid beetles of New Caledonia (Coleoptera: Histeridae). *Fieldiana, Zoology* 37: 601–638, 6 Fig., 3 Pl.

Lighting for Color Photography of Insects

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Through the years photography has become an ever increasingly important taxonomic tool, as its application has become more widespread and as its accuracy has been increased. Color has roughly followed the same pattern as black and white photography; i.e., first it was a crude approximation of the subject, then as the processes were perfected, it became a more exacting tool, until today there are processes which give prints that are almost exact duplicates of the subject.

During the summer of 1951, while photographing insect specimens in some of the various European institutions, it became apparent that one of the key problems confronting the entomological photographer working with color film is the variation in the color temperature balance of the lights and the films. There are several causes for this variation: differences in the voltage, in the length of time the incandescent bulbs have been used, in the age and physical properties of the film, etc. There are several ways that this variation can be solved; some are more accurate than others. The ideal way is to use only fresh film and new bulbs which are designed to operate at the same color temperature, and to have a constant source of electricity, voltage matching that required for the bulbs. Rarely can all of these requirements be maintained for very long.

The main variable factors and their effects are the following: As the voltage decreases, the color temperature of the bulbs also decreases, causing them to become more orange. As the bulbs are used, their color temperature decreases. This effect is very noticeable after only a few hours. Different films are designed to operate at different temperatures: Type A at 3400° Kelvin, Type B at 3200° K., Type F at 3800° K., etc.

In general, there are two ways in which this problem can be handled: adjust the light source either by filters or by changing the voltage of the electricity. Filters are available (Harrison, Eastman, etc.) which correct by increments of 100° Kelvin. For most purposes this will probably suffice, but for accurate color reproduction it does not. The best results can be obtained by using both filters and voltage control; the former for the coarse adjustments and the latter for the finer adjustments.

If one is operating with alternating current and low wattage, it is probably best to use a constant voltage transformer. There are two limiting factors in the use of it: it can only be used with A.C. and the initial cost per watt is very high. Ordinary transformers which are hand adjusted are far less expensive, but these are also limited to A.C. The only way in which one can control the voltage of both A.C. and D.C., and subsequently the color temperature, is with resistance, either with resistors or with rheostats. The only disadvantage to the latter is that they give off heat, but this is not true of transformers.

In order to solve the problem of voltage control, an electrical control panel has been designed and constructed; it is semi-portable, weighing about 75 to 80 lbs. (Fig. 1). The size and the number of meters and switches can be reduced if one desires to operate at only one current and at lower amperage. This one is suitable for operation with the following currents: A.C. or D.C.; 100 to 250 volts; 3 to 55 amps. The voltage can be dropped by 20 to 40 volts depending on the load, and the resulting color temperature of the photoflood lights dropped by about 100° to 200° K., in increments of about 1 to 3° K.

There are four outlets on the left, each with its own cable which can accommodate two sets of lights, from a single bulb to about ten in each set. The main power input cable, a duplex finely stranded number 6, is attached to the lower right. There are a series of end plugs for this input cable that fit the various types of outlets throughout the world. The ground cable, a single finely stranded number 2, is at the upper right. This has an alligator clamp for easy grounding.

Behind the panel the rheostats are mounted in such a way that they are overlapped and staggered to save space. The four-ohm resistors are mounted under the meters, while the two-ohm resistors are mounted in pairs between the rheostats. This arrangement has

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[1] The author wishes to express his thanks to Mr. Marion Klingenberg, Enid, Oklahoma, for his constant efforts to obtain the necessary parts, for technical advice on construction, and especially for the many days spent on the assembling of the panel.

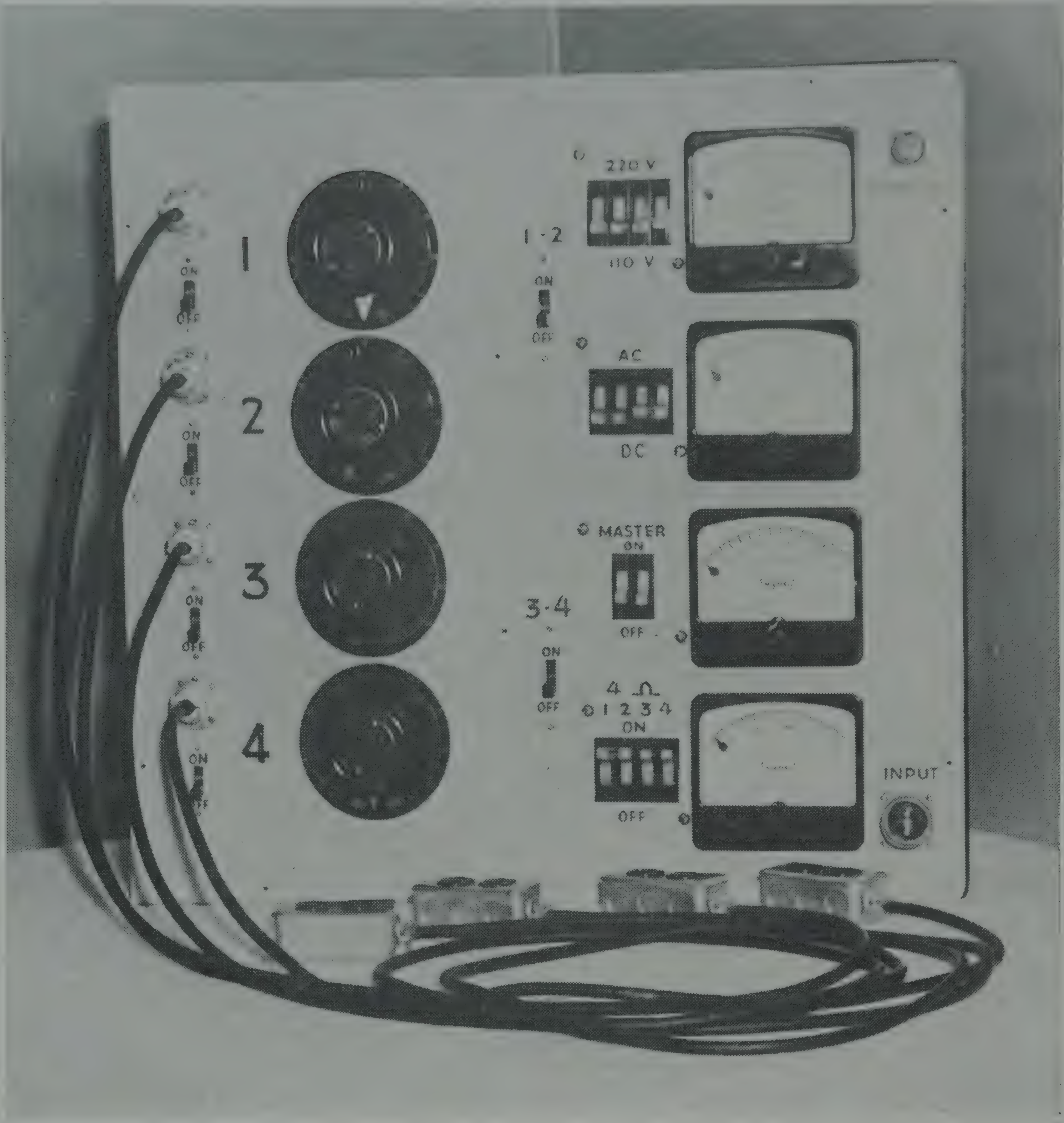

Fig. 1. Electrical control panel.

permitted the front of the panel to be organized in such a way that all switches, meters and knobs are easily accessible.

The basic plan (Fig. 2) is very simple: Resistance is added to the line to change the voltage, which in turn changes the color temperature of the bulbs. Meters record the various currents. Each of the four outlets has its own two-ohm rheostat, two-ohm resistor, and a four-ohm resistor. The latter is equal to the former two; thus if the rheostat and the two-ohm resistor do not pull down the voltage sufficiently, the four-ohm resistor can also be added to the line. A maximum of eight ohms can be thrown into each of the four outlet lines. To make the operation of the panel as simple as possible, whenever feasible the switches have been ganged. For changing from 110 to 220 volts, switches 7, 9, 10 and 11 (the range extender and conversion switches), are ganged, which extends the range of the voltmeter in use and throws output plugs A and B either in parallel or in series with output plugs C and D. For changing from A.C. to D.C. switches 3, 4, 5 and 6 are ganged, placing either the A.C. or D.C. voltmeters and ammeters into the circuit. The master switch consists of two 30 amp., 230 volt switches. A single 60 amp., 230 volt switch would have been used, but as one costs $780., the price was prohibitive.

When constructing such a panel, one should allow several years, as most of the items have to be specially made and the sources of supply for them are difficult to find. All of the resistors were especially made. The cost of such a panel is approximately $1000.

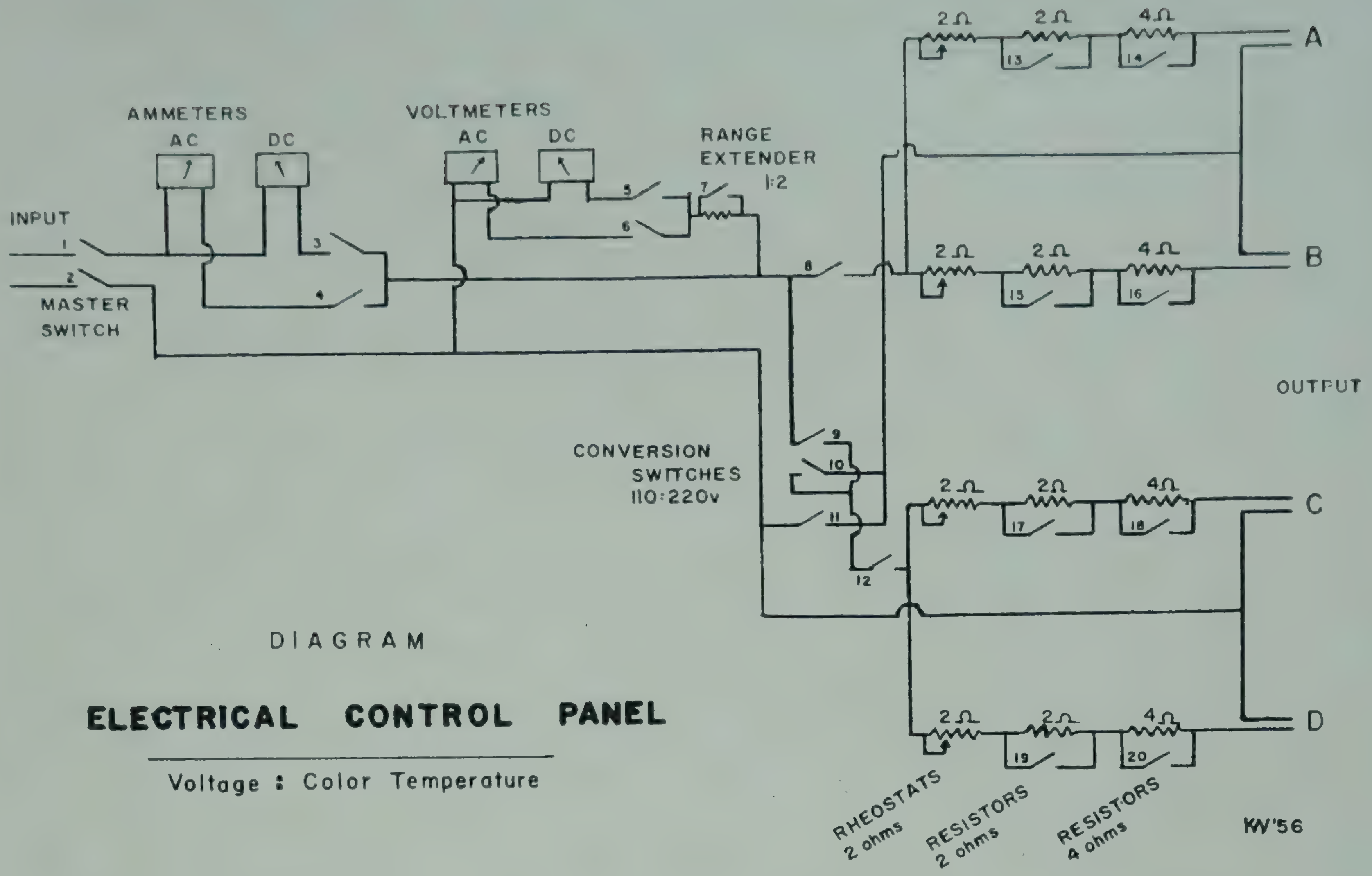
AMMETERS
AC
DC
VOLTMETERS
AC
DC
RANGE
EXTENDER
1:2
INPUT
MASTER
SWITCH
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
2Ω
4Ω
A
B
C
D
OUTPUT
CONVERSION
SWITCHES
110:220v
DIAGRAM
ELECTRICAL CONTROL PANEL
Voltage : Color Temperature
RHEOSTATS
2 ohms
RESISTORS
2 ohms
RESISTORS
4 ohms
KW'56

Fig. 2. Basic plan of electric control panel.

Conclusion: This panel is especially designed to help the photographer obtain a very accurate color balance. For most general work, correction filters are accurate enough; by using them the balance can be off as much as 50° K. Many times when studying color photographs of specimens with questionable color balance, one wishes he could be assured that the colors in the photograph exactly match those of the specimens. When color variation is a key taxonomic character, the accuracy by the panel is essential, merely "good" color balance is not.

Of the three color factors: hue, saturation and lightness, we have been discussing only hue. Saturation is primarily controlled by the film process; hue by the original color of the subject and the color temperature of the illumination. By using the panel and filters it is possible to solve the problem of hue. The problem of saturation is more difficult to solve; most present commercial color film processes have too much saturation. The best color process for our purpose is Agfa. A process has been developed by Curtis using ordinary panchromatic film in a tri-separation camera which allows the photographer to adjust his results for saturation.

As the pigments used in all color film tend to fade, it is best to preserve the results either on black and white film, Curtis process, or to prepare printing plates. At the present time the latter are very expensive, but a process is under development at the Interchemical Corporation using a scanning technique which may greatly reduce the cost per plate.

When accurate color photographs become generally available, it is very likely that color will become a very important taxonomic character, more so than in the past. There is no reason why we cannot study color in the same manner as we study morphological characters.

Quantification of Systematic Relationships and of Phylogenetic Trends[1]

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ABSTRACT

This paper is one of a series demonstrating the application of statistical methods to problems of biological classification. Starting with a table of correlation coefficients between 97 species of bees in the Hoplitis*-complex, tribe Osmiini, family Megachilidae, a series of methods was developed for describing the interrelations of systematic entities. Two methods are presented (the partial correlations method and factor analysis with rotation to simple structure) which give results similar to those of the weighted variable group method (Sokal and Michener, 1957). Certain distinctive features of these methods are discussed. The paper concludes with a second factor analytic method (principal components), which has yielded results which may represent phylogenetic trends.*

CORRELATIONS BETWEEN SPECIES

All the methods described here and in previous publications are employed on a matrix of correlation coefficients among species, based on a number of characters studied for each species. The 97 species in the *Hoplitis* complex which have been used to illustrate these techniques and their characters are discussed in detail elsewhere (Michener and Sokal, 1957). These solitary bees offer an abundance of characters for study and 122 of these were chosen, eliminating all those that were duplicated by being constantly linked with another character. The term "character" is here used to describe an attribute of the organisms varying between species such as color of the abdomen, which occurs in two "states" or alternatives, red and black.

For each character the states were coded: 1, 2, 3 . . . etc. The number of states ranged from 2 to 8; however, most characters had 3, 4 or 5 states with the average number of characters per state at 3.69. The correlation matrix was computed between species (Q-type matrix) using the 122 state-codes for each species as variates. The reasons for this decision and procedural details of computation are described in Sokal and Michener (1957). Correlation coefficients of the product-moment type were computed in preference to other, more appropriate, but computationally more involved coefficients. The computations were carried out by IBM machines and desk calculators and took about two weeks; modern electronic machines, becoming increasingly available, would complete the job in less than one hour.

The 4656 correlation coefficients among the species of our study, resulting from the computation mentioned above, ranged in magnitude from $-.0626$ to $.9747$. When these values were compared with a special series of codes prepared by Michener previous to the start of the statistical analysis, in order to quantify his impressions of the relationships between the species, it was found that they were strongly correlated ($r = .80$). From this and later evidence it could be concluded that the correlation coefficients in the matrix were good indicators of relationships among the species except for certain special cases which are discussed at some length in Michener and Sokal (1957).

ANALYSIS OF CORRELATIONS

Previous Methods

The weighted variable group method was developed by the author with the assistance of C. D. Michener. A detailed description of its rationale and a step-by-step computational outline are presented by Sokal and Michener (1957). The results of the application of this analysis to the *Hoplitis* data are detailed by Michener and Sokal (1957). One outcome of the study was a series of tree-like diagrams of relationship which closely resembled those hypothesized by Michener prior to the study and whose deviations from preconceived relations were often recognized as improved interpretations. While these diagrams as first obtained gave only static, nonhistorical descriptions of relationship, a modification of the method permitted tentative phylogenetic interpretations. A desirable feature of these diagrams is that levels of the forks indicate relationships along a scale at the side of the figure. It should be emphasized that the weighted variable group method is objective in the sense that anyone conversant with the procedure would arrive at the same result, given the identical raw data. It is thus an attempt to remove subjective bias (weighting, value-judgment) from taxonomic procedure.

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[1] Contribution No. 947 from the Department of Entomology, University of Kansas.

[2] The help of Prof. C. D. Michener of the University of Kansas is gratefully acknowledged. Prof. Michener read and criticized the manuscript and furnished much of the information on which this paper is based. Acknowledgement is also due to the University of Kansas General Research Fund for financial assistance.

A part of the research on which this paper is based was performed during the summer of 1956 at the University of Illinois where the author was the holder of a Watkins Faculty Scholarship awarded by the University of Kansas. Appreciation is expressed not only to those responsible for making available this scholarship but also to the following persons at the University of Illinois: Prof. L. H. Lanier for hospitality and facilities in the Psychology Department, Prof. R. B. Cattell for advice on factor analysis and to Mr. John R. Hurley for computational assistance. The computation was performed in part at the Digital Computer Laboratory of the Graduate College of the University of Illinois, thanks to the courtesy of Prof. J. J. Nash, its director. My wife, Julie C. Sokal, helped with computations and illustrations.

Other methods investigated previously included several variations of cluster analysis (Tryon, 1939; Cattell, 1944). These did not give very suitable results since groups formed by these methods generally overlapped, i.e. a given species might be a simultaneous member of two clusters. While this is permissible in abstract schemes of relationship, systematic hierarchic classification must be mutually exclusive at a given level. Newer developments in cluster analysis (particularly by McQuitty, 1955) are being watched with interest. Once some objectionable features can be removed from these methods, their simplicity might easily make them the logical choice for detecting biosystematic group-structure in a matrix of correlations.

The newly applied methods outlined below have been tried out on a small 10x10 matrix (Table I) sampled eclectically from the 97x97 matrix in the *Hoplitis* complex. All

TABLE I. Correlation Coefficients Among the Ten Species Selected from the *Hoplitis*-complex. The Coefficients have been Rounded to Two Decimal Places for Easier Inspection and the Decimal Point has been Omitted.

	SPECIES									
SPECIES	4	5	8	26	35	36	40	50	67	68
4	XX									
5	65	XX								
8	70	84	XX							
26	40	43	49	XX						
35	41	45	49	60	XX					
36	41	42	48	52	94	XX				
40	17	39	44	57	42	29	XX			
50	35	48	52	45	41	33	51	XX		
67	36	37	41	20	25	29	20	49	XX	
68	33	36	43	18	25	29	19	46	96	XX

genera in that group are represented among the ten species studied, but one genus, *Anthocopa*, is represented only by a rather atypical, probably generalized species, *A. copelandica* (Cockerell). The species employed in this study are listed below; they are preceded by the code numbers by which the species are identified in this and other papers.

4. *Proteriades xerophila* (Cockerell),
5. *P. nanula* Timberlake and Michener,
8. *P. cryptanthae* Timberlake and Michener,
26. *Hoplitis louisae* (Cockerell),
35. *H. colei* (Crawford),

36. *H. elongaticeps* Michener,
40. *H. clypeata* (Sladen),
50. *Anthocopa copelandica* (Cockerell),
67. *Ashmeadiella titusi* Michener,
68. *A. femorata* (Michener).

Fig. 1 shows a diagram of relationships for the ten species extracted from the four diagrams (Michener and Sokal, 1957, Figs. 12 to 15) on the relations of all 97 species. It will be used as a criterion for evaluating the methods presented below. Species 5 and 8 belong to the same species-group in the subgenus *Proteriades*. Species 4 is a specialized derivative of the *Proteriades* stem, equally related to the two species-groups in that subgenus, but placed into a subgenus of its own (*Xerosmia*) because of its peculiar features. Together 4, 5 and 8 represent the genus *Proteriades*. The genus *Hoplitis* has four representatives: 26, 35, 36 and 40. Species 26 belongs to the *subgenus Monumetha*, while 35 and 36 are closely related and in the subgenus *Alcidamea*. Species 40 appears to be a very specialized form derived from *Monumetha*; at one time it was placed in a genus by itself and is now the monotypic subgenus *Formicapis*. The third genus, *Anthocopa*, is represented by 50, mentioned above, while the fourth genus *Ashmeadiella*, provided two species, 67 and 68, very closely related members of the subgenus *Ashmeadiella*. By way of a phylogenetic background, it appears that there are two main evolutionary lines in this group, the *Hoplitis-Proteriades* line and the *Anthocopa-Ashmeadiella* line. *Proteriades* appears to have been derived from *Hoplitis*, and *Ashmeadiella* from *Anthocopa*.

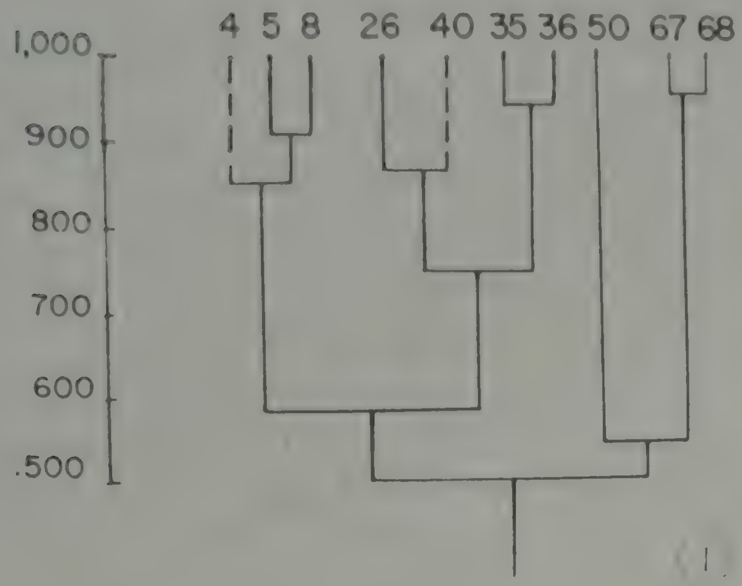
FACTOR ANALYSIS

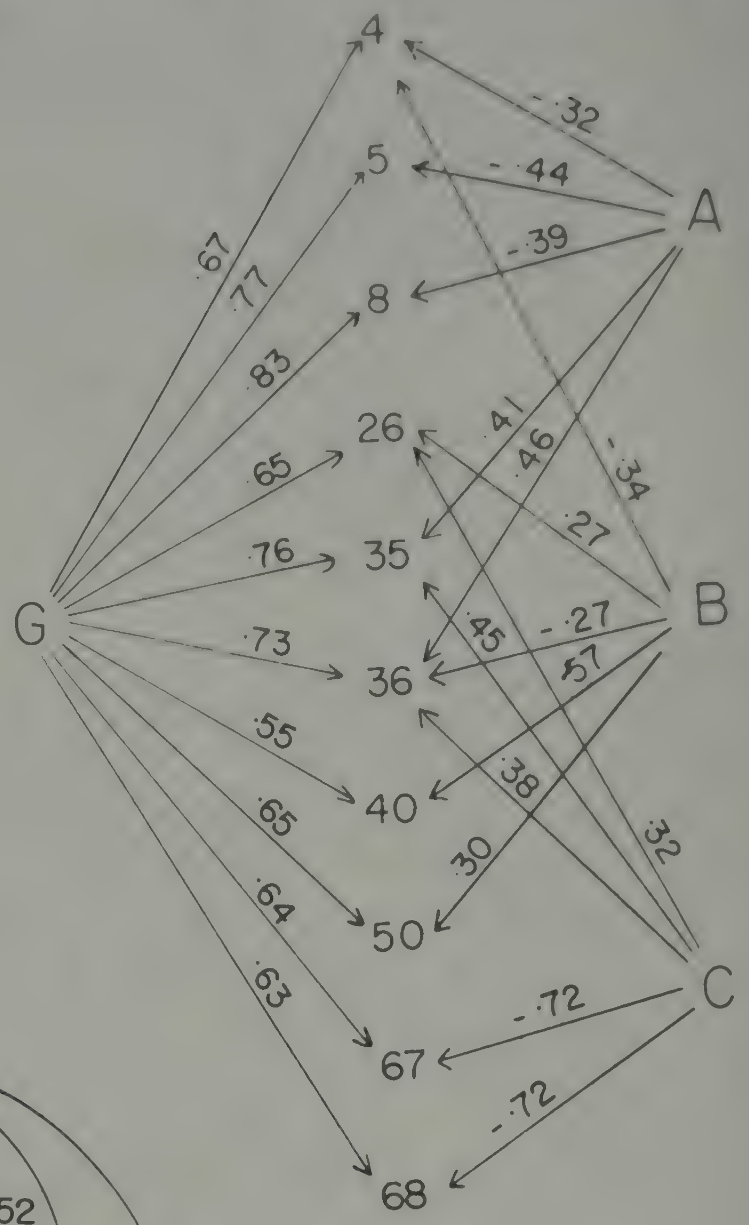
Since the three techniques reported below are all related to factor analysis, a brief introduction to the latter is indicated. Factor analysis is a branch of multivariate statistics which in examining a complex set of phenomena attempts to express these in terms of a few underlying factors, which explain a large part of the variance of the original observations. The raw material of a factor analysis is generally a matrix of correlation coefficients. The customary matrix is one of correlations among characters; in our case the correlations are among species. The factors which emerge from such a study are hypothetical constructs which can frequently be shown to possess objective reality, either through reappearance in successive factor analyses of similar material (invariance) or by positive identification as a known causal factor. We can therefore employ factor analysis with profit when (1) the underlying causes are unknown; (2) the underlying causes cannot be controlled; or (3) when the very nature of the research problem makes control of causal factors undesirable. The results of a factor analysis are presented either in tabular form or by means of arrow diagrams, the method adopted below because of the small size of the matrix. The results show the size of the factor loadings which are standard partial regression coefficients, indicating the amount of dependence of every variable on each single factor, other factors being held constant.

Several procedural steps in factor analysis remain controversial. The number of factors that can or should be extracted from a given matrix cannot as yet be determined with certainty. In the results discussed below four factors have been extracted from the 10x10 matrix. This decision was reached on the basis of the average result of a series of tests for the number of factors. Several distinctly different constellations of factor structure can interpret the identical matrix with comparable degrees of efficiency. Thus there is some controversy over which constellation represents the "true," biological factor pattern. The author will avoid this issue in this paper and merely report the findings of the two most frequently used constellations. Suitable introductory texts for the interested reader are Cattell (1952) and Fruchter (1954).

PARTIAL CORRELATIONS

This technique, patterned after a procedure devised by Wright (1954), employs a modified principal components analysis. Only the first, general factor is extracted from the data. Factor loadings are computed by Hotellings iterative procedure, except that self-correlations (communalities) are reestimated at each iterative step. This assures maximum loadings for the first factor, when other factors need not be extracted. From the newly





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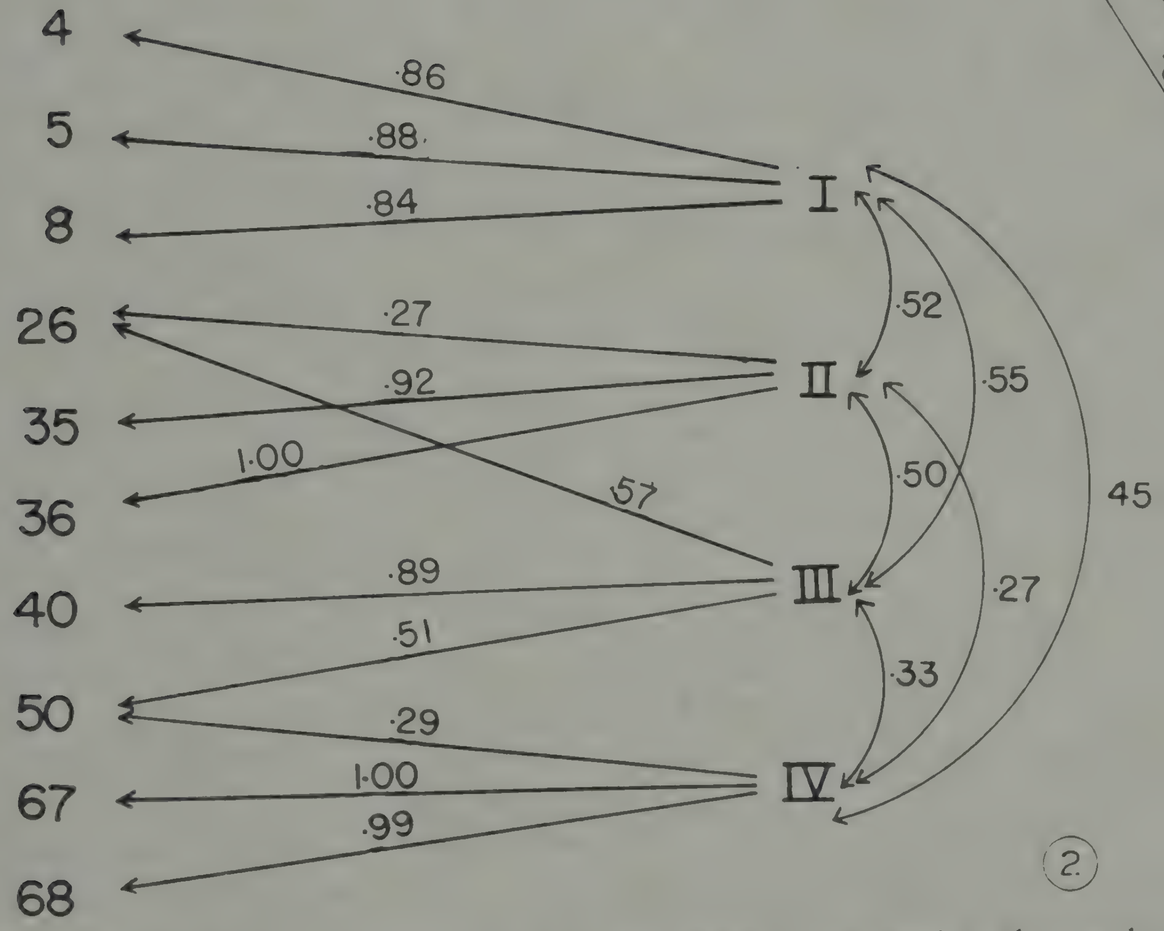

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Fig. 1. Diagram of relationships for the ten species considered in this study, extracted from diagrams on the entire *Hoplitis*-complex shown in Michener and Sokal (1957).

Ordinate: magnitude of correlation coefficient between stems multiplied by one thousand. Broken lines indicate species with an unusually large amount of specialization. By the weighted variable group method species 4 joined stem 5–8 at level 626 in terms of the scale at left, but is shown joining at a higher level since we believe it to be a specialized "exgroup" species (see Michener and Sokal, 1957 and Michener, 1957). Similarly species 40 joined stem 26 at level 568.

Fig. 2. Arrow diagram for first four factors of principal components analysis of correlation matrix among 10 species in the *Hoplitis*-complex (Table I). Factor matrix has been rotated to simple structure. Straight one-way arrows represent factor loadings ("patterns"); magnitude of loading is shown by number above arrow. Arrows for loadings of less than .25 have been omitted in the interest of clarity. Species are identified with Arabic, factors with Roman numerals. Curved two-way arrows indicate correlation between factors. Magnitude of such correlations is shown by numbers to the right of these arrows.

Fig. 3. Arrow diagram for first four factors (unrotated) of principal components analysis of correlation matrix among 10 species in the *Hoplitis*-complex (Table I). Symbolism as in Fig. 2. Since by this method of analysis the factors are uncorrelated there are no two-way arrows in the diagram. The general factor (G) has been drawn to the left of the species in order to avoid too many arrows crossing each other. The other factors are indicated by letters (A, B and C) to avoid confusion with the factors of Fig. 2.

obtained factor loadings and the original correlation matrix a residual matrix is computed. Appropriate correction terms, which take into account the reduced variance after removal of the first factor, can in turn change the residual matrix into a matrix of values analogous to partial correlation coefficients, i.e. they indicate correlation between variables when the general factor has been removed (or kept constant). The author has employed this technique previously on morphological correlations in houseflies (Sokal and Hunter, 1955).

In the present instance removal of the general factor means ignoring all those characters which varied together to make these ten species of bees resemble each other. It also means that the partial correlations are based only on those characters which show correlation among members of smaller groups within the *Hoplitis*-complex. Thus the general factor is a general systematic factor for the complex, or rather for the sample of ten species from it, while the partial correlations show up clusters of relationship above and beyond the general relations.

The partial correlation coefficients among the ten species, with the general factor held constant, are shown in Table II. Comparison with Table I will show that most coefficients have become reduced below .23, the 1% level of significance. When an arbitrary lower limit of .30 is established to indicate important partial r's, four clusters, outlined in the table, emerge. The first cluster defines species 4, 5 and 8. It can clearly be seen that species 4 is related to the other two at a lower level than they are to each other. Other clusters group 26 with 40 and 35 with 36. The close relation between species 67 and 68 is indicated by the high partial coefficient of .95. Absence of any high correlation involving species 50 points out the isolation of that species. Some of the other relations between the stems can be gleaned from an inspection of the lower coefficients. However, relations become less clearcut when we consider these lower values and the method in the following section is to be preferred for a detailed analysis of relationships at higher levels.

TABLE II. Partial Correlation Coefficients (General Factor held Constant) Among the Ten Species Selected from the *Hoplitis*-complex. The Coefficients have been Rounded to Two Decimal Places for Easier Inspection and the Decimal Point has been Omitted. Compare with Table I.

SPECIES	4	5	8	26	35	36	40	50	67	68
4	XXX									
5	32	XXX								
8	36	57	XXX							
26	–02	–13	–12	XXX						
35	–11	–22	–29	27	XXX					
36	–06	–20	–21	14	89	XXX				
40	–27	–02	–02	35	07	–11	XXX			
50	–15	–05	–07	04	–13	–21	25	XXX		
67	–02	–12	–14	–27	–27	–15	–14	19	XXX	
68	–05	–12	–09	–28	–26	–14	–14	16	95	XXX

When compared with the weighted variable group method, the partial correlations technique is at a disadvantage since it only describes the tips of the branches of the relationship diagram, while the former method also shows relations at higher systematic levels. On the other hand partial correlations are subject to tests of statistical significance and such conclusions as are based on this method would therefore carry more weight.

Factor Analysis Rotated to Simple Structure

Next a complete factor analysis of the matrix, rotated to a simple structure constellation, was undertaken. The concept of simple structure (see Thurstone, 1947, or Cattell, 1951) requires that factors influence only some of the variables in each matrix and affect other variables little or not at all. In a simple structure solution we therefore do not find a general factor, but instead find group factors affecting overlapping groups of variables.

Correlation between the factors is permitted and is frequently necessary if simple structure is to be attained. While rotation to simple structure was a very tedious and partly subjective method only a few years ago, the recent development of so-called analytical (i.e. computational) procedures has simplified the process considerably.

The data presented here were first subjected to a principal components factor extraction and the first four factors were rotated analytically using a modification of Thurstone's method (Thurstone, 1953) developed by the author which will be published elsewhere (Sokal, 1958).

The results are depicted in Fig. 2 which shows factor loadings ("patterns" or standard partial regression coefficients) along the arrows from factor to species and correlations between pairs of factors along double-headed arrows connecting the latter. Loadings of less than .25 have been omitted in the interest of clarity.

We find that simple structure has brought about a resolution into systematic units. Factors I, II and IV represent *Proteriades*, *Hoplitis* and *Ashmeadiella* respectively. Factor III cannot be similarly interpreted. It appears that the single atypical representative from *Anthocopa* (species 50) was not sufficient for the analytical method to define a factor. Thus III became a factor representing the *Monumetha* stem and the *Hoplitis* affinities of 50. Affinities of 50 toward *Ashmeadiella*, demonstrated by IV, had already been noted in the earlier variable group study.

The correlations between the factors or systematic units resemble their relations as found in previous studies. Group I is closer to II or III than to IV and II is much closer to III than to IV. It would appear that when used with caution this method can give interesting and reliable information resulting in a classificatory hierarchy. In this connection it should be mentioned that multiple factor analysis provides for a factorization of the factors so that in a larger study a whole hierarchy of systematic entities could be set up. It should be emphasized that both partial correlations as well as simple structure showed the affinities of species 4 to 5 and 6, and species 40 to 26. The weighted variable group method needed a special modification to bring out these relations.

Principal Components Factor Analysis

Factor analysis into principal components is perhaps the most elegant factor analysis from the mathematical point of view. Successive extractions of factors result in maximal loadings and minimal residuals at every step. Geometrically the method finds the principal axes of an ellipsoid formed by a multidimensional scattergram representing the states of the 122 characters for the ten species. Algebraically we are finding the latent roots and latent vectors of the correlation matrix. For the non-mathematician it is important to remember that the factors that emerge are uncorrelated (independent, orthogonal) and that the first factor is a general factor which shows the maximum correlation that can be accounted for by a single common factor. The interpretation of principal component factors has been ambiguous in previous biological or psychological investigations. The present case is no exception, as illustrated in Fig. 3.

The loadings of the general factor indicate the amount to which the individual species resemble the "average" *Hoplitis*-complex member. We find that species 5, 8, 35 and 36 are most typical, and it is no surprise that species 40, the isolated *Formicapis* least resembles the group. The two *Ashmeadiella*, 67 and 68, appear less typical than anticipated. (Anticipation was based on large numbers of species of *Ashmeadiella*. Here, with only two species, it is not surprising to find them atypical). It must be remembered that by an "average" type is meant the average of the ten selected species, not of all members of the *Hoplitis*-complex. Thus the loadings on the general factors differ with the number and kinds of variables put into the correlation matrix. This is a disadvantage of the principal components method stressed by its critics (see Cattell, 1952).

The other three factors are less interpretable. Factor A appears to differentiate *Proteriades* from *Alcidamea*, the former having negative loadings on it while the letter is loaded positively. It might thus appear that it represents a phylogenetic trend which developed in one direction in one subgenus and in the opposite direction in the other one. However, detailed inspection of the character states for the species involved disclosed that at least two separate trends were manifested. The *Proteriades*-distinguishing characters were opposed by neutral ones in *Alcidamea* and vice versa. It could be shown that these neutral character states were more homogeneous in their groups than in the other species of the study and it is for this reason that the two subgenera became opposed to each other on the same factor. Special *Proteriades* characters are the short proboscis and the dense hooked bristles of the proboscis, both of which are features of the *Cryptantha*-visiting species of the genus. Other *Proteriades* features are the rather broad concavity of the first metasomal tergum, not margined by a carina; the absence of a flange on the sixth tergum of the female; the longitudinal ridge on the seventh sternum of the male, etc.

Opposing these in factor A are the several characteristic male antennal features of *Alcidamea* (a subgenus of *Hoplitis*) and the protuberant second sternum. This tendency is reinforced by a number of characters of no discriminating and no obvious adaptive value which assume different values for the two groups of species.

Factor C can be similarly analyzed into *Ashmeadiella* and *Alcidamea* characters opposed by neutral ones, in addition to the non-interpretable characters mentioned above. Factor B appears to consist only of such characters and no meaningful interpretation can be assigned to it.

From the above example it would therefore appear that the chief value of a principal components analysis of a correlation matrix among species is finding the loading on the general systematic factor, which would indicate how "generalized" or "specialized" a given species is in relation to the group in which it is placed. The eventual interpretation of the other principal components factors will need further investigation. At this stage it would appear that rotation to simple structure has provided us with the preferred constellation in terms of taxonomic objectives.

REFERENCES

Cattell, R. B. 1944. A note on correlation clusters and cluster search methods. *Psychometrika* 9: 169–184.

Cattell, R. B. 1952. Factor Analysis. *Harper and Brothers*, New York.

Fruchter, B. 1954. Introduction to factor analysis. *D. Van Nostrand Co.*, New York.

McQuitty, L. L. 1955. A method of pattern analysis for isolating topological and dimensional constructs. Research Report AFPTRC–TN–55–62, Air Force Personnel and Training Center, Lackland Air Force Base, San Antonio, Texas.

Michener, C. D. 1957. Some bases for higher categories in classification. *Systematic Zoology* 6: 160–173.

Michener, C. D., and R. R. Sokal. 1957. A quantitative approach to a problem in classification. *Evolution* 11: 130–162.

Sokal, R. R. 1958. Thurstone's analytical method for simple structure and a mass modification thereof. *Psychometrika* 23: (In press).

Sokal, R. R., and P. E. Hunter. 1955. A morphometric analysis of DDT-resistant and non-resistant house fly strains. *Ann. Ent. Soc. America* 48: 499–507.

Sokal, R. R., and C. D. Michener. 1957. A statistical method for evaluating systematic relationships. *Kansas Univ. Science Bull.* 38: 1409–1438.

Stroud, C. P. 1953. An application of factor analysis to the systematics of *Kalotermes*. *Systematic Zoology* 2:

Thurstone, L. L. 1954. An analytical method for simple structure. *Psychometrika* 19: 173–194.

Thurstone, L. L. 1957. Multiple factor analysis. *University of Chicago Press*, Chicago.

Tryon, R. C. 1939. Cluster analysis. *Edwards Bros.*, Ann Arbor, Mich.

Wright, S. 1954. The interpretation of multivariate systems. *In* Statistics and mathematics in biology. *Iowa State College Press*, Ames, Iowa. (Edited by O. Kempthorne).

DISCUSSION

O. W. RICHARDS. Can you justify the arbitrary weighting of characters and then treating such arbitrary numbers by ordinary statistical processes?

R. R. SOKAL. Yes, since the overwhelming majority of applications of statistics do not fully conform to the theoretical assumptions postulated when the statistics were developed. The acceptable values of the correlation coefficients demonstrate their worth empirically. This is not to say that some nonparametric statistic of association may not be preferable in future work.

W. L. BROWN, JR. Would not allometric differences of an extreme sort cause trouble in scoring?

R. R. SOKAL. Yes, but we do not believe that we have such cases in our material.

Insects: Designs in Photography

By Fred P. Roullard
Fresno State College
Fresno, Calif.

ABSTRACT

The creation of geometric patterns by the use of insects in a photographic process is described in this paper.

An 8 x 10 inch printing frame is fitted with a special two-part back consisting of a "stator" and "rotor", which permits multiple exposures of the subject in a radial pattern.

Both apparatus and designs are demonstrated.

Man has long been amazed by the precision and perfection of nature—the beauty of the building of a crystal of so common a thing as salt; the infinite variety and absolute perfection of snowflakes.

Quite by accident, in 1936, I stumbled upon a way to make similar precise and beautiful designs by using another of nature's materials—insects.

The possibilities for the fashioning of designs in this way seem almost limitless, and the experimenter will be enthralled by the charm and mathematical beauty of his creations, each one of which is in itself unique.

PROCESS

The process involved is simply the creating of geometric designs on sensitized paper by repeated exposures of a bilaterally symmetrical form in a radial pattern.

APPARATUS

To accomplish this purpose all that is needed is a regular 8 x 10 inch printing frame, the spring back of which is removed and replaced by a special device. This device consists of a "stator", a fixed back of three-quarter inch wood-stock, to fit the printing frame, and a "rotor", a movable disk of the same material and thickness approximately 7½ inches in diameter.

The stator is divided into equal segments or degrees of any desired number, and an arrow indicator on the rotor permits the accurate measurement of as many sectors as desired.

METHOD

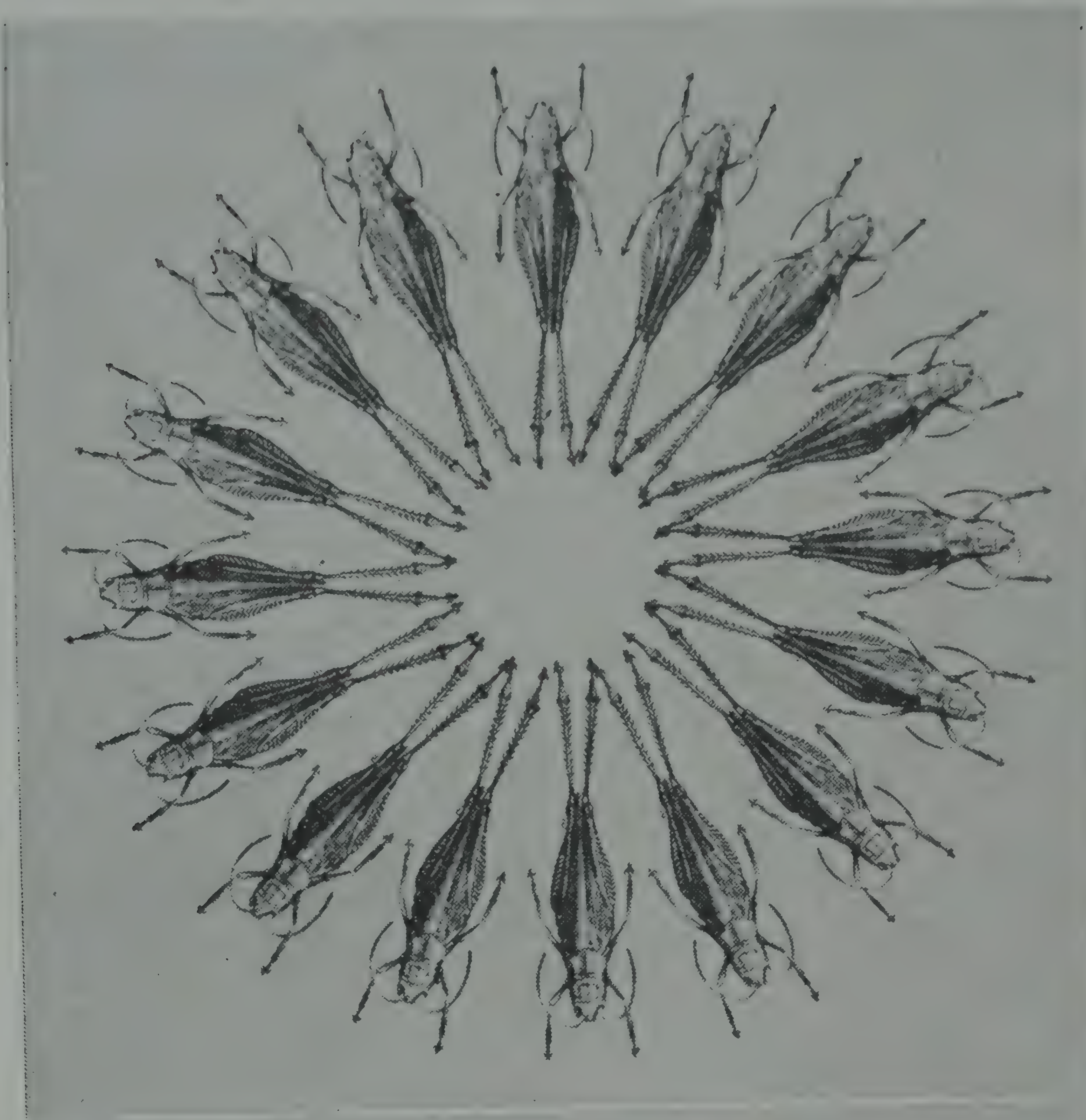
Sensitized paper is mounted, emulsion side up, on the rotor (with art corners for printing). The negative is located off-center and taped to an opaque paper mask with an open space large enough to permit a full print of the subject—grasshopper, butterfly, or other insect. The axis of symmetry of the insect must be in line with the radius of the circle.

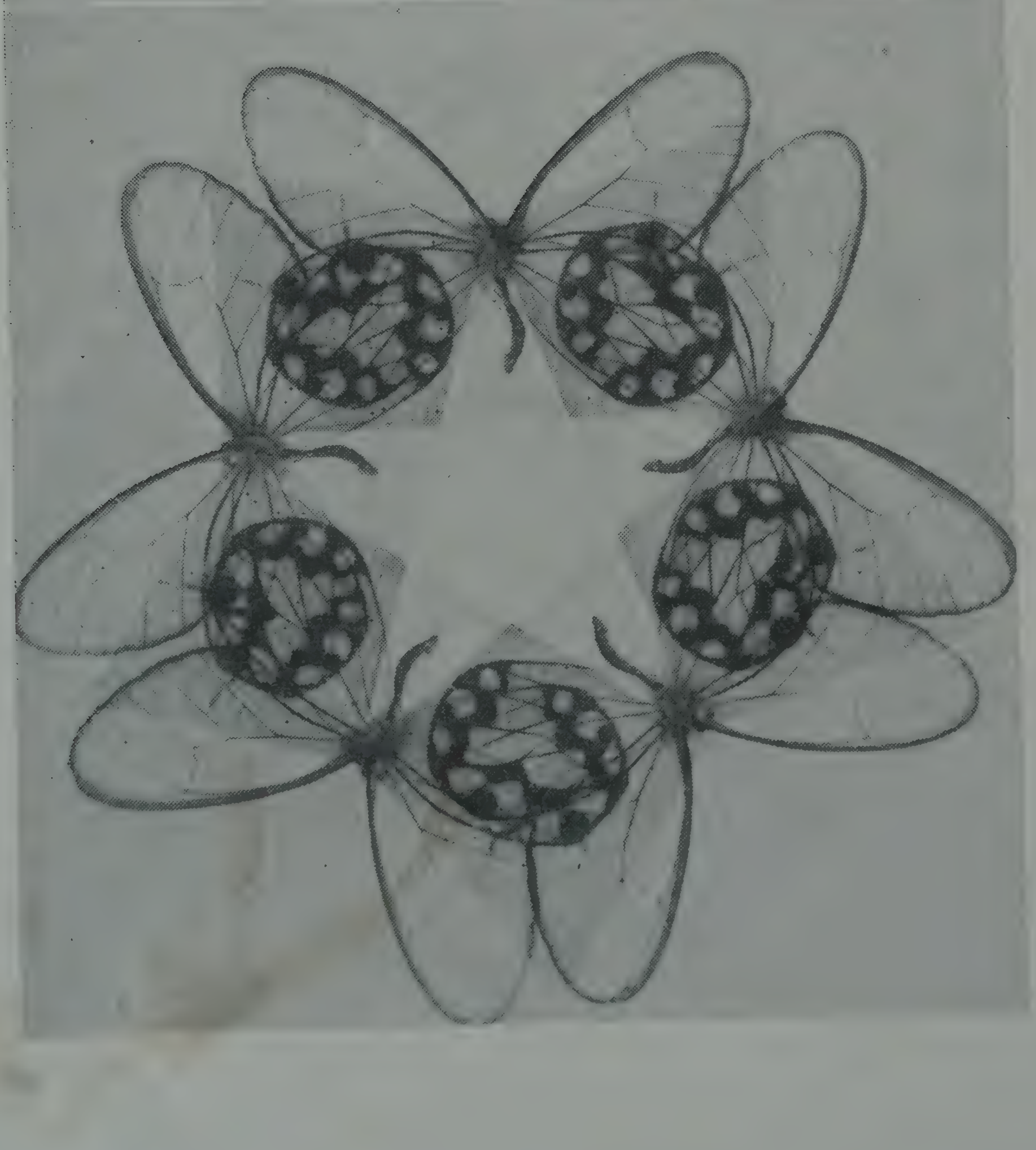
The first exposure is made with the indicator at the first graduation. The rotor is then turned to the next sector mark for the second exposure, and so on until the desired number of exposures has been made. After exposure is completed, the sensitized paper is developed just as usual.

A few of the designs, created by the method given, are shown here, and a model of the apparatus is also available for examination.

Please understand that the apparatus is entirely experimental, and is offered simply as a basis for the further development of a precision printing frame and the more exact techniques which are indispensable in modern color-printing.

Furthermore, I shall make no attempt here to correlate this paper with any of the practical purposes of economic or systematic entomology. Since appreciation of art in nature is an end in itself, I offer it to you, my colleagues, for the pure pleasure it may bring you.





Entomology and Philately

By A. S. RAO
Department of Agriculture
Andhra Pradesh, India

ABSTRACT

The first stamp with insect motif was issued in 1842, hardly 2 years after the birth of the postage stamp. In spite of this the number of stamps bearing insect subjects is now just about a hundred. These were issued by twenty-three countries: British Honduras, Bulgaria, Cameroun, Chile, Czeckoslovakia, Finland, Hungary, India, Italian Somaliland, Mozambique, Netherlands, Panama, Portuguese Guinea, Roumania, Sarawak, Spain, Spanish Guinea, Sweden, Switzerland, Togoland, Trieste, United States, and Yugoslavia. Most of the stamps feature insects, except Roumania (showing a farmer treating his crop), India (malaria control) and Cameroun (commemorating work on sleeping sickness). Unlike medical philately, workers have not been honoured, nor have important events been commemorated. The possibility and necessity of utilising this popular and instructive medium for depicting the contribution of entomology to human welfare is pointed out, since much has been done in this direction in other fields of human activity.

It is nearly 116 years since Roland Hill brought out the first postage stamp. During this period, philately has passed through many changes, reflecting great developments in layout and printing, issue, and sale of stamps. The recent trend in the field of collecting has been the so-called thematic motif or specialised collection, wherein the interest is devoted to a particular category of stamps. Of such may be mentioned, notably, medicine, aviation, railways, sport, art, religion and architecture. Those of natural science include flowers, birds, fruit, fish, and insects.

There is very little mention of insect stamps even in recent entomological literature. Among the standard works, only Frost (General entomology, 1942) lists a single reference. This article (Montgomery, 1937) is revealing in that it states that stamps with the insect motif were issued as early as 1842, barely two years after the first stamp was brought out. Some details of stamps listed by Montgomery are furnished below.

COUNTRY	DENOMINATION	INSECT
Hungary	10–feller and 50 feller surcharge.	bee-hive
U.S.A.	"Penny Post"	bee-hive
U.S.A. (1842)	1 and 2 cents	bee-hive
Italian Somaliland (1932)	1.5, 1.75, and 2 lire	termite nest
Spain (1934)	15 centimos	cockroach or beetle (?)

Since 1934, twenty countries have issued insect stamps. These are: British Honduras, Bulgaria, Cameroun, Chile, Czeckoslavakia, Finland, Hungary, India, Mozambique, Netherlands, Panama, Portuguese, Guinea, Roumania, Sarawak, Spanish Guinea, Sweden, Switzerland, Togoland, Trieste, and Yugoslavia. All these add up to about a hundred stamps. There are in the author's collection about 40, details of which are furnished below:

HUNGARY. A set of 10 stamps (4 vertical and 6 horizontal) was issued in 1954. The insects are on a background of their host-plant or habitat. (currency 100 filler = 1 forint).

DENOMINATION	INSECT
30 fi	turnip beetle
40 fi	crawling cockchafer
50 fi	greater capricorn beetle
60 fi	hornet on grapes
80 fi	Apple beetle (weevil)
1 fo	Corn Beetle
1 fo 20	Black cricket
1 fo 50	Rhinoceros beetle
2 fo	Stag beetle
3 fo	Water beetle

INDIA (currency 16 annas = 1 Rupee). A single stamp was issued in the series representing the different aspects of the first five-year plan which ended this year, wherein great importance was attached to malaria control. The stamp is oblong and of 6 annas denomination. The left side shows a village with a marshy pond in foreground on which an anopheline mosquito is superimposed, and on the right half a well laid-out scene showing factories. The Aesculapian symbol interposed between the two scenes represents the knowledge, medical and entomological, that is making this transformation possible.

PORTUGUESE GUINEA. A set of 10 stamps was issued in 1953 with various insects in natural colours.

DENOMINATION	INSECT
5 centavo	blister beetle (*Analeptes trifasciata*)
10 centavo	bug (*Callidea panaethiopica*)
30 centavo	beetle (*Craspedophorus brevicollis*)

SPANISH GUINEA. A set of 4 vertical stamps was issued on colonial stamp day in 1953. The butterfly stamps have a plant in flower in the background.

DENOMINATION	INSECT
15 Centimos	beetle (*Trogocephala nobilis*)
60 ”	butterfly (*Papilio antimachus*)
5 +5 ”	beetle (*Trogocephala nobilis*)
10+5 ”	butterfly (*Papilio antimachus*)

MOZAMBIQUE. A set of twenty stamps depicting various butterflies and moths of this Portuguese colony in East Africa was issued in 1953. Except for one stamp (1 escudo), all are oblong. This is one of the finest set of insect stamps issued so far, both pictorially and entomologically.

DENOMINATION	INSECT
10 centavos	*Papilio demodocus* Esp.
15 ”	*Amphicallia thelwalli* Drc.
20 ”	*Euxanthe wakefieldi* Ward.
30 ”	*Axiocerses harpase* F.
40 ”	*Teracolus omphale* God.
50 ”	*Papilio dardanus tibullus* Kirb.
1–00	*Aigenia mimosae* Bsd.
2–00	*Athletes ethica* Westw.
2–50	*Papilio phorcas ansorger* Rtsch.
3–00	*Arniocera ericata* Btlr.
4–50	*Egybolis viallantina* Stoll.
6–00	*Xanthospilopteryx mozambica* Mab.
10–00	*Charaxes azota* Hew.

CZECKOSLOVAKIA. There are in my collection 2 oblong stamps, one of 30 heller depicting a stag beetle on a pink background and another of 1–40 h. with a butterfly (*Papilio* sp?) on a light yellow background.

SARAWAK. Sarawak is represented by a single stamp issued in 1950, 1 cent in denomination, and bearing King George VI inset and the butterfly *Troides brookiana*. Sarawak is a British crown colony on North coast of Borneo.

SWITZERLAND. Since 1950 Switzerland has been issuing stamps for children's welfare, and in many cases insect motifs have been chosen. Up to 1954 19 stamps had been released. The stamps have in the background plant leaves and flowers. The following seven are with the author:

DENOMINATION	INSECT
10+10 (1951)	dragonfly
20+10 (1951)	swallow tail butterfly
10+10 (1952)	lady bird beetle
20+10 (1952)	butterfly
10+10 (1953)	moth
20+10 (1953)	butterfly
10+10 (1954)	tiger moth

The other stamps issued are: 1950 (red admiral butterfly, moth, bee and sulfur butterfly), 1951 (orange tip butterfly and emperor moth), 1952 (blue butterfly and oak egger moth), 1953 (purple longicorn beetle) and 1954 (buff-tailed humble-bee, fly, and butterfly).

Cameroun. A single large oblong stamps was issued by this French colony in Africa to commemorate the 75th anniversary of Dr. Jamot Vainqueur (1879–1954), whose bust is reproduced on the stamp. Also shown is an improvised laboratory with workers at their job, flanked on either side by a tse-tse fly. Though this stamp is not colourful, it finely recaptures the efforts of a pioneer who worked for the control of sleeping sickness.

Sweden. This country has issued a stamp in honour of Linneaus, the great biologist.

The details of insect stamps from other countries are given below:

Country	Insect
Panama (1948)	mosquito
Roumania (1947) and (1955)	bee-hive, farmer treating his crops, against pests
Togo (1954)	goliath beetle
Trieste (1950)	bees, silkworm
Yugoslavia (1954)	black beetle, grasshopper
Netherlands	baby and bees, girl and butterfly
British Honduras	butterfly
Bulgaria (1940–41)	bee-hive, bee keeping
Chile (1948)	insects
Finland (1954)	dragonfly, bees collecting pollen, butterfly

From the information presented above, it is clear that, during the last two decades, the use of insect motif on stamps has increased considerably. Most of them feature insects —mostly butterflies, and moths, followed by beetles, bugs, flies, and bees. These, beautiful as they are, do not represent the contribution of the entomologist to the welfare of his country and the world. Pioneers have yet to be honoured, events commemorated, and land marks of entomological progress made more widely known through this medium. In other fields the stamp has been more effectively utilised. A notable example is medicine wherein thematic collection from among stamps of medical interest is now possible (Pleones, 1954). As I see it, there are great possibilities of popularising entomology, if only we get more interested in these little ambassadors.

REFERENCES

Frost, S. W. 1942. General entomology. p. 61.
Gibbon. 1956. Simplified stamp catalogue of the world.
Montgomery, B. E. 1937. Insect stamps. *Ent. News* 48: 184.
Ploenes, W. 1954. Medicine and philately. *Medical Mirror* 5: 1. (Darmstadt, Germany).

The Relationships of Systematics and the Principles of Organic Evolution

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ABSTRACT

Evolutionary studies to date have stressed variables that can be studied in laboratory experiments or by studies of subspeciation. There is a great group of variables yet to be discovered that can be explored best through phylogenetic analyses, especially in the level between species and families. Some of this has been done using paleontological material, but fossil material does not have sufficient associated ecological and biological data to give much of the picture. This field, which may be called field evolution, can best be explored through the avenue of systematic studies combining paleontological and neontological material, in which phylogeny, biology, and ecology can be correlated into a unified evolutionary whole. Examples are given from various groups of insects illustrating methods by which some of these correlations have been attempted.

First let us examine the second phrase of the title of this article, "the principles of organic evolution." Evolution is a process, not a science. It is the dynamic process involving change and time, which has produced the several million kinds of organisms now inhabiting the earth. In studying this process practically all our inquiries resolve themselves into four questions: What happened, when did it happen, how did it happen, why did it happen? If we accept as a definition for the word "principle" the concept of a general truth or proposition, then we can say that any general truth or axiom which we can learn concerning either the what, when, how, or why of evolution, can be regarded as one of evolution's principles. I would like to probe the possibilities of systematics contributing to such principles.

To begin with, I doubt if anyone would ever have formulated the idea of an orderly evolution of organisms, that is, the initial "what" of evolution, if it had not been for systematics. Before the units of evolution, the species, could be studied, they had to receive a name or handle, and be arranged in some orderly system in which similarities and differences were expressed. Thus the eighteenth century system of binomial nomenclature and its later superstructure of orders and classes provided a background against which observations from comparative anatomy, embryology, and other disciplines could be arranged and brought into synthetic focus.

This original organization necessary for the realization of the existence of evolution was essentially the development of a concept of phylogeny. Following publication of the early works on evolution, many systematists worked out phylogenetic schemes for a great number of animal and plant groups based on the comparative anatomy of living forms. In a considerable number of these attempts the material was meagre, some of the observations were erroneous, or the reasoning was faulty, leading to conclusions which were soon proven incorrect. It is regrettable that due to this circumstance plus the inordinate faith put by many in paleontology and genetics as the sole expositors of evolution, phylogeny by the neontologist became descredited and slipped into somnolescence. Only in comparatively recent years has the deduction of phylogeny again come to attract the attention of the systematist. It is now clear that it was impossible for phylogeny, any more than for physics or any other science, to produce perfect newborn products and ideas, but that these must be continually improved through discovery of better information and methods of interpretation.

It is becoming equally clear that phylogeny is the means through which the systematist can make the greatest contributions to an understanding of the process of evolution, either by unearthing questions for another science to answer, or by making observations or deductions concerning ideas of general application.

There is a good reason why the systematist dealing with living forms occupies such an important position with regard to phylogeny. As groups are studied more carefully it is found that more and more detailed characters are needed to establish the exact relationships of allied forms. Many of the needed characters are seldom or never preserved in fossils, as for instance the baculus in mammals (White 1953) and the musculature in birds (Beecher 1953). In the insects needed characters may be distributed through several life history stages, which are seldom found associated as fossils, or may be minute characters such as setal patterns, proportions of leg or palpal segments, shape of tentorium, or many others which are invisible or not preserved in fossil remains. It is not my intention to disparage the study of fossils, rather to point out the necessity of combining information from both living and fossil specimens, and the reliance which must be placed by the phylogenist on living forms for extremely important data.

In many insect groups a sufficient number of species have survived to portray in detail the course of evolution, such as with the *borealis* group of the caddisfly genus *Helicopsyche*, Fig. 1. This initial phylogenetic diagram alone expresses certain data concerning evolution, namely, what characters changed, how much they changed, and the degree of difference between related species. Because we know this detailed information for a relatively small number of groups in comparison with the total for the world, either plant or animal, it is reasonable to expect new ideas to come from learning more about these simple aspects of emergent evolution.

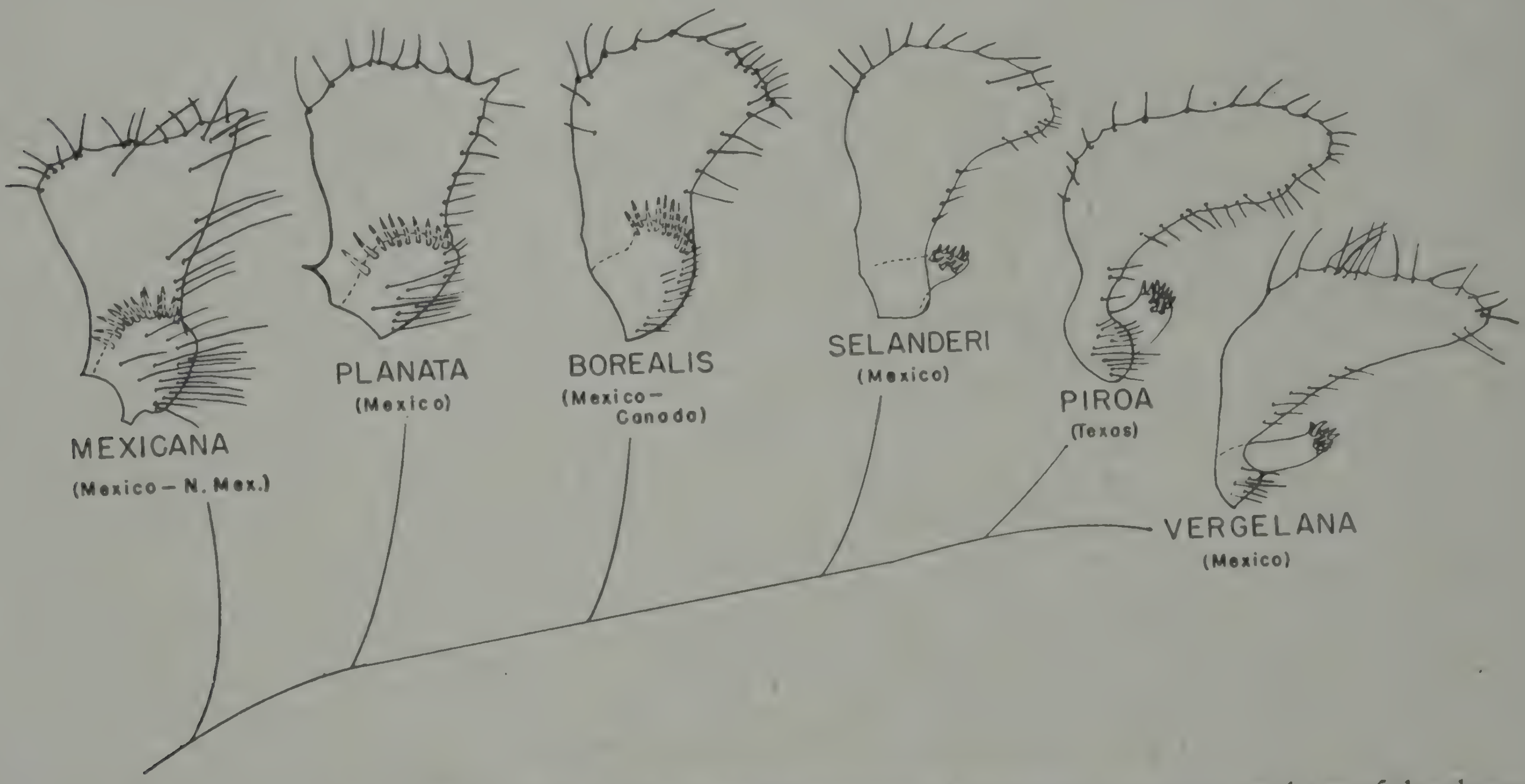

Fig. 1. Family tree of the *borealis* branch of the genus *Helicopsyche*, showing the evolution in shape of the clasper from the primitive species *mexicana* to the specialized species *vergelana*.

If various biological, ecological, or geographic data concerning the species are added to these simple family trees, other conclusions may be drawn. In Fig. 1, for instance, the range of each species is indicated. Five of the six species have a small range but *borealis* extends northeastward far beyond the range of all its congeners. This fact tells us that in some fashion this species has developed an ecological tolerance much wider than any of its relatives. This same phenomenon, that is, one member of a complex or genus possessing an unusually wide ecological tolerance, occurs frequently in insects. Examples include the caddisfly, *Oecetis inconspicua*, the sawflies, *Neodiprion abietis* and *Dolerus similis*, and the leafhopper, *Macrosteles fascifrons*. The genetic basis or mode of origin of these unusual species is yet unexplained, but these species may play a role of unsuspected importance in various phases of the evolutionary process.

Biogeography is another aspect of evolutionary study to which systematics can contribute. It is now well recognized that various groups of organisms have spread from one part of the world to another at various times in the past. This has resulted in a constant mixing of the elements of the biotic communities ever since such biotas came into existence. It is further recognized that all groups of organisms did not disperse at the same time, and that few dispersed in exactly the same way. This leads us to the conclusion that one of the most important factors in the genesis and composition of our present biotic communities has been this highly variable dispersal pattern of organisms.

Our knowledge of these dispersal patterns is at present very rudimentary. Because of the tremendous number of species involved, and because of the extraordinary variety of ecological types they represent, insects will be of the greatest aid in the discovery of whatever order is in these dispersal patterns. Insect fossils will be of great help in adding chronological data but are relatively few in number. The great bulk of the data that insects will contribute to dispersal concepts will come from the systematics of neontological forms, through correlating geographical distribution with phylogenetic analyses. Several gross types of dispersal pattern have already been established. In one type, exemplified by the caddisfly genus *Sortosa*, Fig. 2, an ancient form became widespread as early as the Cretaceous, resulting in the subsequent establishment of various evolutionary lines, many of which have remained isolated on different continents ever since. In the case of *Sortosa*, at least eight such restricted units are known, involving inhabitants of every continental mass. In another type of dispersal, isolated elements have evolved into lines having presumably different ecological properties than their sister lines, and have subsequently redispersed to many parts of the world. Such a redispersal is well illustrated by the genus *Chimarra*, a specialized offshoot of *Sortosa*, which appears to have originated in South America and afterwards dispersed to many parts of the world. Major dispersal routes of *Chimarra* are shown by the thin lines in Fig. 2. Leafhoppers of the genus *Erythroneura* show a dispersal pattern similar in many ways to that of *Chimarra* (Ross 1953).

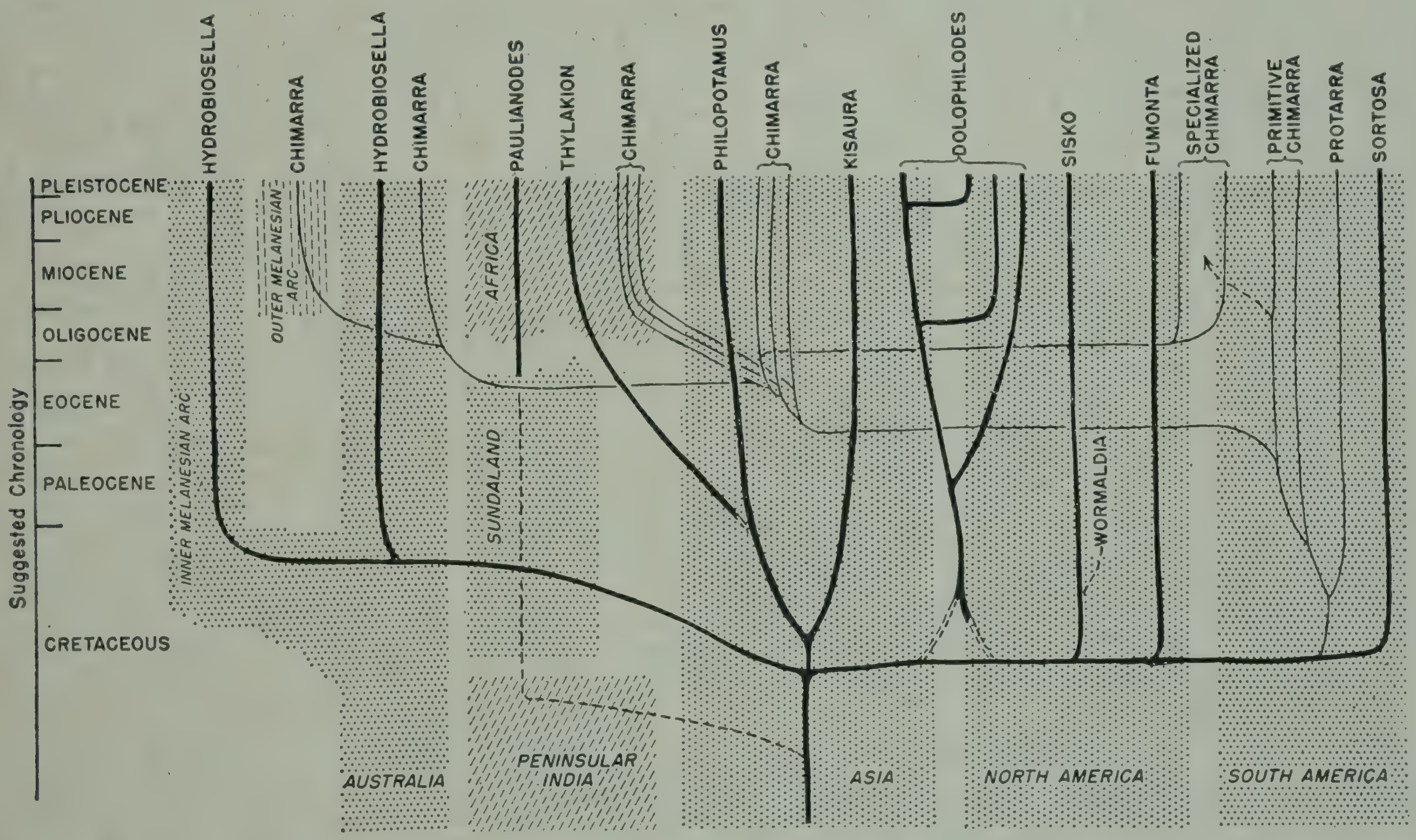
HYDROBIOSELLA
CHIMARRA
HYDROBIOSELLA
CHIMARRA
PAULIANODES
THYLAKION
CHIMARRA
PHILOPOTAMUS
CHIMARRA
KISAURA
DOLOPHILODES
SISKO
FUMONTA
SPECIALIZED CHIMARRA
PRIMITIVE CHIMARRA
PROTARRA
SORTOSA
Suggested Chronology
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
CRETACEOUS
INNER MELANESIAN ARC
OUTER MELANESIAN ARC
AFRICA
SUNDALAND
WORMALDIA
AUSTRALIA
PENINSULAR INDIA
ASIA
NORTH AMERICA
SOUTH AMERICA

Fig. 2. Phylogenetic dispersal chart of the genus *Sortosa* and its primitive allies (indicated by the wide black lines) and *Chimarra* and its allies (indicated by the thin lines). (After Ross 1956).

In still another type, intercontinental dispersal appears to have occurred frequently in relatively recent geologic times, resulting in an unusual taxonomic heterogeneity of the fauna in each area. An example is the leafhopper genus *Macrosteles*. In this genus it is necessary to postulate about twenty dispersals between North America and Eurasia in order to explain the relationships and present distribution of the known world fauna of *Macrosteles* (Moore and Ross 1957). It is evident that these intercontinental dispersals have been much more numerous and more recent than in the case of either *Sortosa* or *Chimarra*.

All four of these examples represent different ecological types. *Sortosa* is a dweller in cold, rapid streams; *Chimarra* is primarily an inhabitant of warm, rapid streams; *Erythroneura* is a warm temperate to subtropical terrestrial genus which feeds on shrubs and trees; and *Macrosteles* is primarily a warm to cool temperate genus which feeds on grasses and herbs. These characteristics of the insects add to the store of information concerning the ecological nature of the land bridges between continents or other isolated areas over which the insects dispersed. The number of insect groups which can be studied in this fashion is tremendous, and in total represents many duplications of practically every shade of ecological difference to be found in the terrestrial and fresh-water world. I have every confidence that when the dispersal patterns are known for a sufficiently large number of diverse insect groups, we will be able through comparison and elimination to deduce the exact ecological characteristics of every major land bridge occurring in the last hundred million years.

A lively controversy has been going on for some time concerning the circumstances under which species multiplication takes place, particularly in the case of animals. In what manner does one species split up to produce two or more species? Some writers claim that this phenomenon occurs only by geographic isolation of segregated portions of species populations, whereas others believe that various types of ecological isolation may produce the same result without geographic separation of populations. To date cited examples of ecological isolation are open to much question. On this problem the insect systematist can obtain valuable data. Some findings from the leafhopper genus *Erythroneura* illustrate one way in which this can be done.

Primitive members of the genus *Erythroneura* occur in both the Old and New Worlds. Biogeographic evidence (Ross 1953) indicates that a series of specialized branches developed in the Old World and that populations of one of these, the *obliqua* group, dispersed to and became established in the New World. The progeny of this population evolved into about five distinctive branches, including the *comes* group, the *maculata* group, and the New World portion of the *obliqua* group. The New World evolution of these branches appears to have occurred almost entirely in the eastern deciduous forest of North America after this forest had become isolated ecologically from western forest areas during mid-Tertiary time, about 40 million years ago. This monophyletic cluster of *Erythroneura* branches, which presumably started out 40 million years ago as only one or at most a few species, today totals about 350 species.

Several other insect groups appear to have become isolated in North America at the same time. These groups also appear to have dispersed into eastern North America when the temperate deciduous forest was Holarctic in distribution, to have been isolated in the eastern deciduous forest when this was isolated in mid-Tertiary, and to have evolved as species flocks essentially restricted to the area until the present time. At present these groups have evolved into the following known number of species: *Taxonus* 9, *Neodiprion lecontei* group 14 (sawflies), and *Pycnopsyche* 19, *Neophylax* 15, *Hydropsyche scalaris* group 18, *Agapetus* eastern branch 14 (caddisflies). The average number of species is 15, in tremendous contrast to the 350 species known for the eastern development of *Erythroneura*. What evolutionary factor or factors account for this unusually high rate of species multiplication in *Erythroneura?*

The most obvious factor concerns the matter of hosts. In most known cases, each species of *Erythroneura* breeds on only one species of host plant or on a group of closely related host species. To date some 50 shrub and tree host species have been established, distributed in 30 genera, 19 families, and 12 orders of plants. Because even the plant genera are much older than mid-Tertiary, it is obvious that the leafhoppers did not become associated with this wide range of plants by the process of evolving as the plant lines evolved, but must have become established on various plant genera long after these came into existence.

In the next few illustrations I have charted the host relationships on the family trees of two of these recent groups of *Erythroneura*. In the case of the 43 species of the *comes* group, Fig. 3, it is obvious that, except for the most primitive branch on *Cornus*, the entire line had a base or ancestral host of *Vitis* and its allies. From this ancestral host we have evidence of five host transfers, one to *Salix*, one to *Hamamelis*, and three to *Cercis*.

In Fig. 4 are shown the host relationships and phylogenetic arrangement for the species complexes of the *maculata* group. The large number of phyletic lines (for some of which hosts have not yet been associated) makes this appear extremely complicated, but the unusually frequent occurrence of oak hosts in the lower part of the tree suggests that *Quercus* was the ancestral host and that many of the lines now occurring on other trees arose from *Quercus*-inhabiting ancestors. Using the same type of reasoning, the specialized cluster of branches shown at the top of the chart appears to have evolved from a *Corylus*-

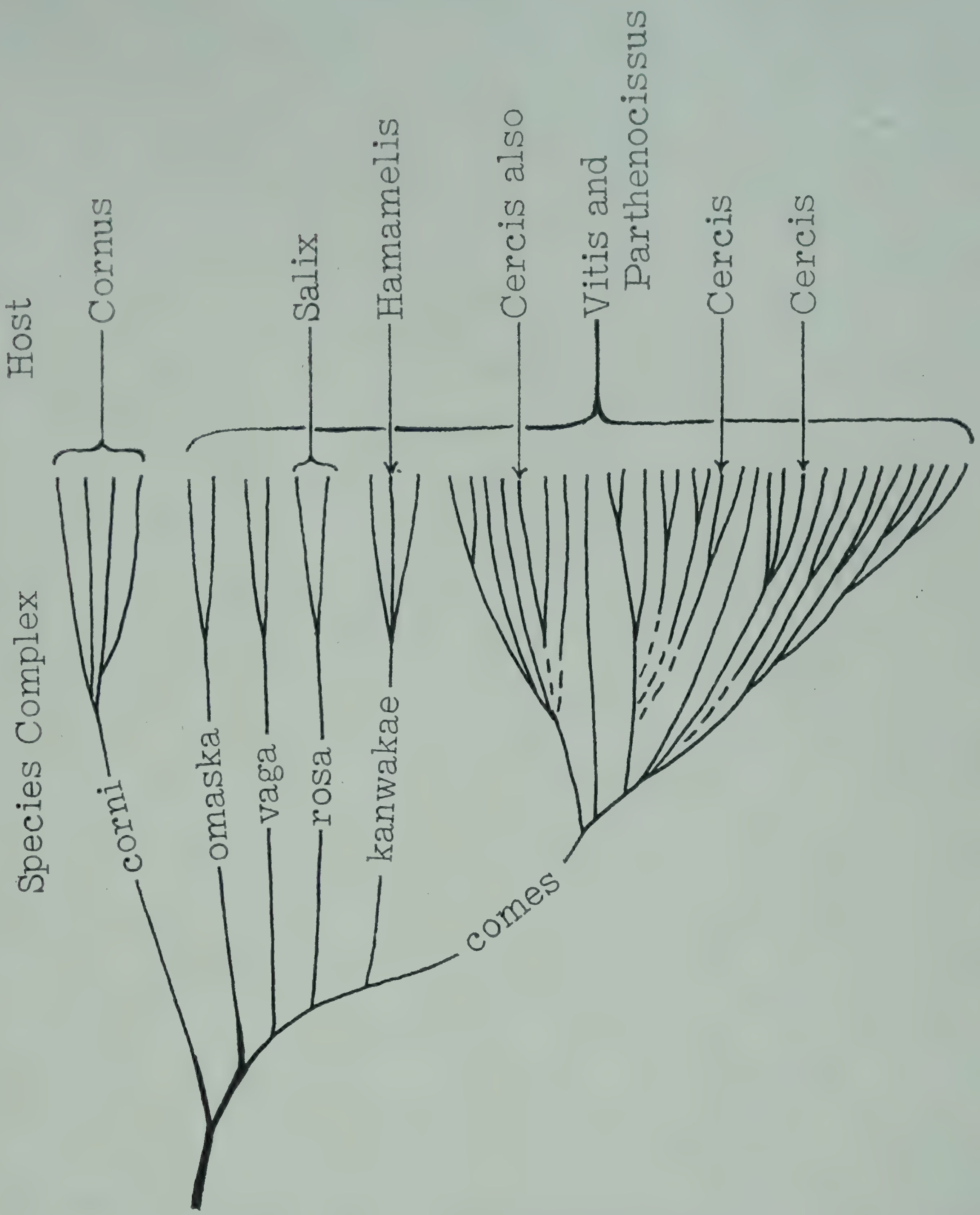

Fig. 3. Phylogenetic tree of the *comes* group of the leafhopper genus *Erythroneura*, and its hosts. Species names of the leafhoppers have been omitted but each line represents one species.

inhabiting ancestor. This idea is expressed more graphically in Fig. 5. Whether our surmises are correct or not regarding *Quercus* being the ancestral host, the data on this chart show conclusively that at least 27 intergeneric host transfers were made during the evolution of this group.

Known host data from these two charts and from American members of the *obliqua* group of *Erythroneura* indicate that about 150 host transfers have occurred in these three branches of the genus, spread over some 40 to 60 million years, or an average of one transfer every quarter or third of a million years.

It seems reasonable to conclude that the unusually large number of *Erythroneura* species occurring in the eastern deciduous forest has been produced through a host transfer process. Presumably at various times a few specimens or a larger population of a particular species became established on a new host, became conditioned to the new host, and in this way began a new phyletic column independent of the parental populations in a genetic and evolutionary sense.

In these few examples concerning the role of systematics in elucidating evolutionary thought, systematics itself enters into the logic. I would like to point out another type of investigation in which systematics forms only the background and not part of the logic for the argument, but nevertheless a type of investigation for which the systematist is frequently the only qualified observer. These are investigations along the borderline between systematics and ecology, or systematics and genetics, and so forth.

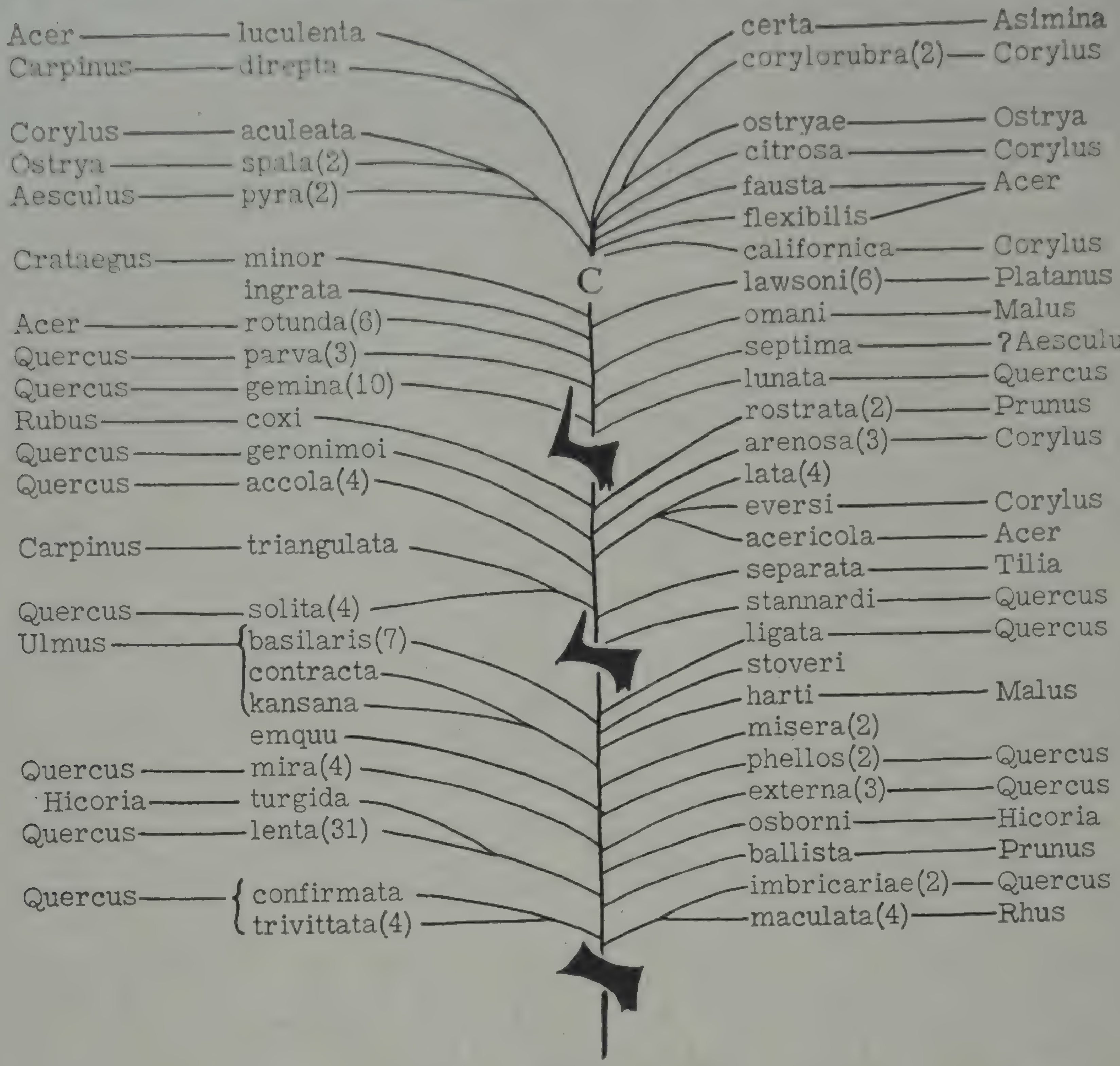
Acer luculenta
Carpinus direpta
Corylus aculeata
Ostrya spala(2)
Aesculus pyra(2)
Crataegus minor
ingrata
Acer rotunda(6)
Quercus parva(3)
Quercus gemina(10)
Rubus coxi
Quercus geronimoi
Quercus accola(4)
Carpinus triangulata
Quercus solita(4)
Ulmus basilaris(7)
contracta
kansana
emquu
Quercus mira(4)
Hicoria turgida
Quercus lenta(31)
Quercus confirmata
trivittata(4)
C
certa Asimina
corylorubra(2) Corylus
ostryae Ostrya
citrosa Corylus
fausta Acer
flexibilis
californica Corylus
lawsoni(6) Platanus
omani Malus
septima ?Aesculus
lunata Quercus
rostrata(2) Prunus
arenosa(3) Corylus
lata(4)
eversi Corylus
acericola Acer
separata Tilia
stannardi Quercus
ligata Quercus
stoveri
harti Malus
misera(2)
phellos(2) Quercus
externa(3) Quercus
osborni Hicoria
ballista Prunus
imbricariae(2) Quercus
maculata(4) Rhus

Fig. 4. Family tree of the species complexes of the *maculata* group of *Erythroneura*, with the known host indicated. The letter C indicates an apparent ancestral form occurring on *Corylus*. The black figures indicate the progressive changes in the style of the male genitalia.

As an example I would like to cite recent studies involving the so-called Gause's law. As expressed by Lack (1949), this law is interpreted to mean that more than one species cannot inhabit and utilize the same ecological niche at the same time. For some time many cases have been known to insect systematists in which several species appeared to be utilizing the same niche simultaneously. Two of these cases have recently been analyzed, one by Dr. Usinger, reported in our Monday morning session, and another concerning a group of six species of *Erythroneura* which coexist on the eastern sycamore *Platanus occidentalis* (Ross 1957).

The existence of groups of species utilizing the same niche jointly seems to be adequately confirmed, and suggests that, at least with the insects, this is a common phenomenon governed by a complex set of natural forces, chief of which are the absolute size of the organisms and the climatic variability of the niche.

It is of interest that these studies corroborate certain of the ecological premises employed by Andrewartha and Birch (1955). It is of further interest that these studies will also require a reorientation of the thinking of many evolutionists concerning the subjects of competition, species survival, and, as a corollary, a reconsideration of various aspects of natural selection.

The detection of such cases hinges on the search on the part of the systematist for adequate series and samples to elucidate a taxonomic problem, and the prosecution of each case frequently involves the use of taxonomic techniques and characters with which the non-systematist is unfamiliar. The most conclusive cases of coexistence involve groups of

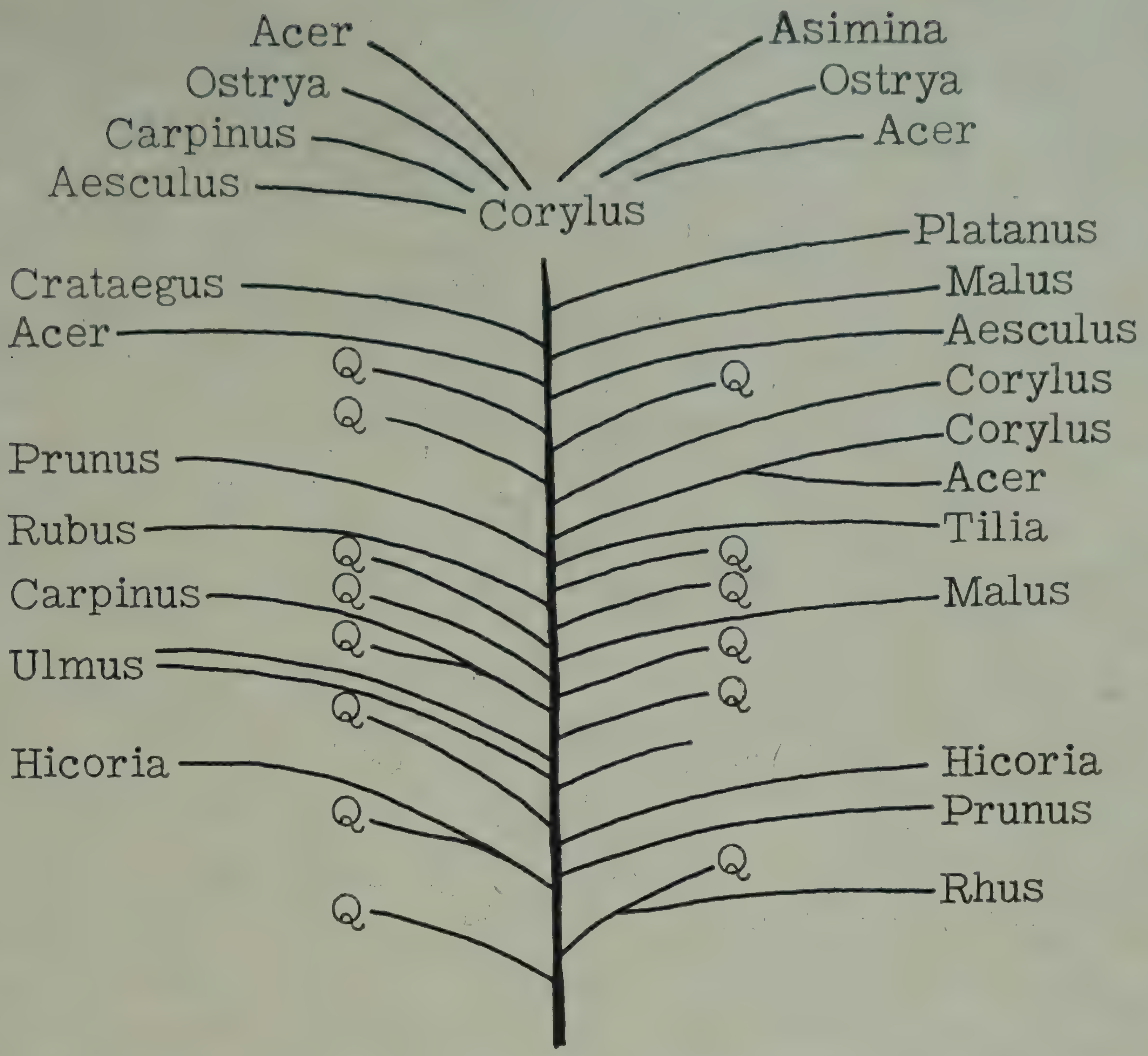

Fig. 5. Same as Fig. 4 but with the names of the species complexes omitted and the apparent ancestral host *Quercus* indicated by the letter Q.

closely related species, since such species usually have similar habits and similar demands on the environment. Thus even here the phylogenetic approach is a real aid in detecting and evaluating problems.

Returning to the relationships of systematics and the principles of evolution I believe we can set forth a few general points. Systematics deals with and attempts to define the products of evolution. Through the field of phylogeny it attempts to reconstruct the course of evolution. It would be surprising if a science so intimately interwoven with the fabric of evolution would not also lead to the elucidation of important concepts of evolution. The examples just given, which cover only a few of the topics which might be cited, seem to illustrate that such contributions by systematics are indeed possible, comprising either answers to some of the questions concerning the evolutionary process, or the formulation of new pertinent questions which must be answered in genetics, ecology, geology, or some other field.

We can become so absorbed in finding the answers to questions that we tend to neglect the importance of discovering new questions, and without new questions we can make no continued scientific progress. It is unimportant that the questions arising in one field concern another, providing that they eventually come to the attention of the pertinent discipline.

REFERENCES

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. *Univ. of Chicago Press.* 782 pp.
Beecher, W. J. 1953. A phylogeny of the Oscines. *Auk* 70: 270–333.
Lack, D. 1949. Darwin's finches. *Cambridge University Press*, London. 208 pp.
Moore, T. E., and H. H. Ross. 1957. The Illinois species of *Macrosteles*, with an evolutionary outline of the genus. *Annals Ent. Soc. Amer.* 50: 109–118.
Ross, H. H. 1953. On the origin and composition of the nearctic insect fauna. *Evolution* 7: 145–158.
Ross, H. H. 1956. The evolution and classification of the mountain caddisflies. *Univ. of Illinois Press*, Urbana, Ill. 213 pp.
Ross, H. H. 1957. Principles of natural coexistence indicated by leafhopper populations. *Evolution* 11:113–129.
White, J. A. 1953. Genera and subgenera of chipmunks. *Univ. Kans. Publ., Mus. Nat. Hist.* 5(32): 543–561.

Our Knowledge of the Insects of the Pacific Islands[1]

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ABSTRACT

The insects of the Pacific islands are very unequally known. Some areas have been intensively collected, but the collections very little studied. The faunae of Hawaii, New Zealand, and Japan may be the best known. Many of the old collections are in the British Museum or in other European museums; Bishop Museum has the most extensive collections from many island groups, such as Micronesia, Hawaii, Marquesas, Samoa, Fiji, and southeastern Polynesia—most of the oceanic Pacific islands. Many of these collections have hardly been studied. The museum is now publishing the Insects of Micronesia series, and from time to time publishes papers on Fiji or elsewhere. The richer continental islands, such as New Guinea, the Bismarcks, Solomons, and Indonesia require much further attention, both for field work and taxonomic research, before the faunae become at all adequately known.

Since the earliest voyages of discovery, naturalists have demonstrated a great fascination for the study of life on the scattered islands of the Pacific. However, even to the present date, many island groups have been inadequately collected for insects, and the faunae of still more are very incompletely studied. The birds, plants, and other groups are in general better known than the insects.

The insular environments offer unparalleled opportunities for limitless research in various phases of zoogeography, evolution, ecology, and genetics. Insect populations can be studied under various conditions of low populations, isolation, relative absence of predators, parasites, or competitors, or under competition in limited environments, and they could be compared with related populations on continental islands or continents. The phases of dispersal to, and establishment and persistence upon, isolated islands, need much study. Obviously before these phases can be reported upon to any extent, the classification of the species must be achieved. Field work on the Pacific islands is expensive and time-consuming because of the great distances involved, the multiplicity of islands, and the problems of transportation. Bishop Museum is interested in furthering the knowledge of the Pacific island insect fauna, and we hope that adequate means may be found to accomplish both this and the research in evolution and ecology suggested. The opportunities for this research are fast disappearing in many island groups because of the despoiling of nature by the increase or shifting in human populations and the commercial exploitation for everything from phosphate mining, lumbering, and coconut and cacao plantations to airports and military bases, not to mention the spread of species by increasing air travel to the further extermination of native fauna. Many interesting species are being lost today because of the elimination of their limited niches.

The insect faunae of the island groups are quite unequally known. Those of Hawaii, the Marquesas, Samoa, and New Caledonia are fairly well known, at least in many groups of insects. Those from the Micronesian island groups are receiving considerable attention at the present time, and island groups like the New Hebrides, Santa Cruz Islands, Tonga, New Guinea, the Bismarck Archipelago, and the Solomons have been very inadequately collected and studied. As the faunae of the outlying island groups are quantitatively and qualitatively poorer, some of the least known areas are by far the richest in fauna.

Early contributions to the knowledge of insects of the Pacific islands resulted from fragmentary collections made by naturalists of the early voyages. Among these were those of d'Entrecasteaux, 1791–93; Captain Kotzebue, 1817; Captain Freycinet, 1819; Le Seniavine, 1823; La Coquille, 1824; l'Astrolabe, 1828; the Beagle, 1835–36, South Polar Voyage, 1837–40; the Eugenie, 1851–53; the Novara, 1857–59; the Marchesa, 1883. Then there were various administrators and planters, mostly German, who collected in Micronesia,

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[1] Continental Asiatic islands are excluded.

Samoa, the Solomons, Bismarcks, and New Guinea. Various expeditions, from the middle of the past century down to the present, added much knowledge. Among them were those of Wallace in 1858; Netherlands government New Guinea expeditions of 1903 and later dates; Templeton-Crocker expedition (California Academy of Sciences), 1923; Whitney South Sea expedition (American Museum of Natural History), 1921–37; St. George Expedition (British Museum), late 1920s; Pacific Entomological Survey (Bishop Museum), 1929–32; Mangarevan Expedition (Bishop Museum), 1934; Caroline Island Expedition (Bishop Museum), 1936; T. Esaki's Micronesian expeditions (1936–40); Archbold expeditions (five to New Guinea, one to Queensland), 1934–1956; and others.

Some of the individual entomologists who made significant collections are listed, following, by island groups. *Hawaii*: Blackburn, Perkins, Giffard, Muir, Swezey, Zimmerman, Hardy. *Marquesas Is.*: Whitney South Sea expedition, St. George expedition, Pacific Entomological Survey (Adamson, Mumford, LeBronnec). *Society, Austral, Cook, and Mangarevan Islands, and Rapa*: St. George expedition (Cheesman), Mangarevan expedition (Zimmerman), Krauss. *Samoa*: various Germans, Buxton, Hopkins, Harris, Swezey, Zimmerman, Hoyt, Krauss, Gressitt. *Tonga*: fragmentary collections, Galathea expedition, Krauss. *Fiji*: Mann, Paine, Tothill, Lever, Simmonds, Veitch, Bryan, Zimmerman, Kondo, Krauss, Gressitt. *Gilberts*: Catala, Moul. *Marshalls*: Esaki, Wallace, Usinger, La Rivers, Beardsley. *Carolines*: Esaki, Yasumatsu, Ono, Kondo, Dybas, Townes, Oakley, Gressitt, Maehler, Goss, Adams, Potts, Clarke, Beardsley. *Mariana Is.*: Esaki, Swezey, Usinger, Oakley, G. Bohart, Gressitt, Dybas, R. Bohart, Townes, Maehler, Krauss. *Bonins*: Kuwana, Furukawa, Mead, Kondo, R. Bohart. *New Zealand*: many collectors, Tillyard, Broun, Salmon, etc. *New Caledonia*: Deplanche, Savés, Viette, Cohic, Crabb. *New Hebrides*: Cheesman, Whitney South Sea expedition, Bauer, Krauss, Laird. *Solomons*: Whitney South Sea expedition, Mann, Paine, Tothill, Lever, Franclemont, Gurney, Rheimscheissel, Beck, Brown, Gressitt, Ford. *Bismarcks*: various Germans, Froggatt, O'Connor, Dun, Szent-Ivany, Ardley, Gressitt, Ford. *New Guinea*: Wallace, Finsch, d'Albertis, Tryon, Hagen, Biro, Macleay, Wollaston, Meek, Eichhorn, Pratt, Stevens, Cheesman, Modigliani, Le Roux, Stüber, Archbold expeditions, Toxopeus, Lieftinck, Boschma, Pemberton, Issiki, Bronggersma, Holthuis, MacMillan, McNamara, Ross, Hoogstraal, Malkin, Jewett, Krombein, Darlington, Brandt, Szent-Ivany, Wilson, Gressitt, Ford, Dodd, Woodward.

The museums where major collections are housed are listed following by areas. *Hawaii*: Bishop Museum, British Museum. *Marquesas Is.*: Bishop Museum. *Southeastern Polynesia*: Bishop Museum. *Samoa*: Bishop Museum, British Museum. *Tonga*: British Museum, Bishop Museum. *Fiji*: Bishop Museum, British Museum. *Micronesia*: Bishop Museum, United States National Museum, Chicago Natural History Museum, Kyushu University, California Academy of Sciences, Museum of Comparative Zoology. *New Zealand*: British Museum, Canterbury Museum, University of New Zealand, Bishop Museum. *New Caledonia*: Bruxelles Museum, Paris Museum, Bishop Museum, United States National Museum, British Museum. *New Hebrides*: British Museum, Bishop Museum. *Solomons*: British Museum, Bishop Museum, Berlin Museum, United States National Museum, American Museum of Natural History. *Bismarcks*: Bishop Museum, British Museum, Berlin Museum. *New Guinea*: Leiden Museum, Bishop Museum, British Museum, United States National Museum, Amsterdam Museum, Australian Museum, South Australian Museum, Berlin Museum, Museum of Comparative Zoology, California Academy of Sciences, Chicago Natural History Museum, Budapest Museum, Genoa Museum, Paris Museum, Riksmuseum, American Museum of Natural History, Bogor Museum, Taiwan University, University of Queensland, Department of Agriculture, Stock and Fisheries at Port Moresby.

Some rough estimates of numbers of species known from the various island groups, together with guesses as to the probable endemicity and percentage of species known from each group, are presented in the following table.

TABLE I. Estimates of Pacific Island Insects.

Island group	Species named	Total fauna	Percentage of endemicity
Hawaii	4,000	10,000	98
Marquesas Is.	900	2,000	60
SE Polynesia	1,100	3,000	60
Samoa	1,850	6,000	60
Tonga	300	1,800	30
Fiji	2,800	25,000	90
Bonins	300	1,000	60
Mariana Is.	1,000	3,500	55
Carolines	1,000	6,000	65
Marshalls–Gilberts	250	1,200	5
New Zealand	6,000	15,000	90
New Caledonia	2,000	7,000	90
New Hebrides	1,000	5,000	85
Solomons	2,500	25,000	80
Bismarcks	1,800	15,000	65
New Guinea	5,000	40,000	80

Taxonomist's Glossary of Genitalia in Insects

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ABSTRACT

At the Congress in Amsterdam in 1951, I proposed that a glossary on the outer genitalia in insects be compiled. This book is now ready.[1]

The word outer was removed from the title as it could not be unanimously delimited, the stress being laid upon the purpose of the work, viz., to be an aid to taxonomists, and the authors were given a free hand to include as much or as little of the "inner" genitalia as they found suited.

Thirty-four specialists contributed to the general description, compilation and explanation of the terms. The first part of the book contains descriptions of the "outer" genitalia of the 29 orders of insects; the second part is a list of terms attached to these genitalia. This comprises more than 4000 terms arranged as main words or as synonyms, with all possible cross-references and with definitions of the main words.

The terms are given in their original form in English, French, German or Latin, a few also in Italian and other languages. The inflection of the Latin words is given. The book in this way should be not only a scientific aid for morphologists and taxonomists but also a linguistic one.

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[1] Taxonomist's Glossary of Genitalia in Insects. Edited by S. L. Tuxen. *Ejnar Munksgaard*, Copenhagen. 1956.

Sur la Validation et l'Usage du Terme Topohomoeotype[1]

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RÉSUMÉ

Il apparaît de plus en plus désirable qu'un courant d'échanges de spécimens clés devant servir à la taxonomie soit mis en marche de facon sérieuse et amplifiée constamment entre les diverses institutions dépositaires de matériel type entomologique et dont la principale participation à cette discipline zoologique est la systématique.

Le topohomoeotype peut très bien combler cette lacune des impossibilités d'accès au matériel type primaire dont la nécessité toujours de plus en plus grande est maintenant reconnue par tous les savants entomologistes; à ce titre, le topohomoeotype devrait être considéré, bien que n'étant pas de la catégorie des types primaires, comme un suppléant à rang égal et conséquemment supérieur à tout autre matériel type du groupe secondaire. La désignation d'un tel matériel type doit cependant rencontrer les exigences des règlements et opinions qui régissent la sélection du matériel type et être en tous points conforme aux données déjà établies ou à établir par la Commission internationale de Nomenclature zoologique.

Après plus de vingt ans d'une constante liaison avec les Musées d'Histoire ou de Sciences naturelles et les Musées mixtes, il nous faut encore s'étonner en constatant le nombre de conservateurs de musées de sciences, d'entomologistes et autres savants pour qui, les mots "SPÉCIMENS-TYPES" et ce qu'ils représentent sont valeur insignifiante.

Pour ces collègues de musées de sciences ou musées mixtes tout comme pour un grand nombre d'entomologistes, il apparaît évident que la consécration de quelques pages d'une brochure à ce problème des spécimens-types est une perte d'argent et de temps. Si cette incompréhension est excusable chez un profane il est, par contre, fort difficile de concevoir un tel état d'esprit chez les gens de profession.

C'est pour rappeler ce problème que l'ICOM ou Conseil International des Musées, avec le concours financier de l'UNESCO, publia, en 1955, un opuscule traitant de ce sujet. Nous avons nous-mêmes, au Musée de la province de Québec, publié en même temps un mémoire concernant les problèmes de gardiennage de matériel type et quelques considérations générales sur les difficultés que rencontrent les dépositaires de spécimens-types entomologiques.

Dans le travail du Comité de l'ICOM dont les résultats ont été rédigés par le Dr. W.-E. Swinton du British Museum of Natural History pour la plus grande utilité des musées de sciences naturelles, nous sommes particulièrement heureux d'y trouver la sanction de pratiques et de méthodes que nous préconisons et appliquons au Musée de la province de Québec, sur un plan un peu plus amplifié cependant, depuis plus de quinze ans.

Nous sommes parfaitement d'accord avec les membres du Comité de l'ICOM sur le fait que notre génération s'estime fort supérieure aux précédentes en jugement et en capacités et que naturellement, cette estimation, qui pour autant qu'elle peut être méritée ne manque néanmoins pas d'une certaine suffisance, nous amène de temps à autre à remettre en question les bases de notre science zoologique.

Ceci, bien entendu, ne peut se faire qu'en étudiant, à la lumière du progrès général de la science, les documents originaux qui sont à la base des diverses sciences. L'historien et l'archiviste ont nécessité de documents originaux pour leur travail; les spécimens-types sont les documents originaux du naturaliste. Mais voilà . . . où trouver ces documents originaux aujourd'hui?

Nous demeurons toujours d'accord avec le Comité de l'ICOM sur le problème que présente, par le temps et par la négligence de conservateurs non-spécialisés de musées de sciences, la perte effarante d'une quantité de matériel type.

Nous sommes disposés à convenir qu'il est presque impossible, dans notre ère atomique, de parer à tous les dangers sans exception, les risques de guerre entraînant une destruction rapide demeurent toujours, mais nous n'hésitons pas à affirmer qu'il est quand même possible de réduire ces risques et dangers à un rigoureux minimum.

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[1] A déjà paru dans *Le Naturaliste Canadien* 84(2): 62–68. 1957.

Dans un travail d’amorce préparé en 1954 que nous avons présenté aux entomologistes du Canada lors du Congrès national tenu à Frédéricton, Nouveau-Brunswick, à l’automne 1955, nous en arrivions, sans être encore au courant des résultats de l’étude du Comité de l’ICOM, à des constatations identiques quant à la nécessité urgente et à l’importance vitale pour les musées eux-mêmes et pour les diverses institutions scientifiques à fournir un inventaire catalogué de leurs collections zoologiques.

Ce devoir impérieux englobe nécessairement l’idée d’une conservation technique, d’une signalisation adéquate et uniforme en même temps que l’application de mesures aptes à résoudre le plus efficacement possible les problèmes d’inaccessibilité que présente aux chercheurs une localisation éparse de spécimens-types dans les grands et petits musées du monde.

Nous avons déjà, dans un mémoire du Musée de la province de Québec, exposé nos vues sur la conception d’une conservation technique et nous y avons fait connaître les méthodes que nous avons appliquées en entomologie. Nous n’avons pas craint d’y déplorer vivement la perte de quelques spécimens-types de 1900 à 1930 alors que l’institution n’était encore qu’un musée scolaire. N’allons pas croire cependant que seuls les moyens ou petits musées de sciences ou les musées mixtes ont cette nécessité de l’application urgente et immédiate d’une conservation technique? De grands musées nationaux ont perdu des quantités fort appréciables de spécimens-types pour diverses raisons mais le plus souvent, malheureusement, par la négligence de conservateurs insuffisamment compétents ou intéressés en d’autres sphères.

Combien parmi les grands musées nationaux d’Europe possèdent encore un seul spécimen ornithologique du XVIII^e siècle? Et pourtant certains de ces musées sont plus que deux fois centenaires! On peut compter sur les doigts d’une seule main les musées nord-américains qui ont en collection un exemplaire du Canard du Labrador (*Camptolaimus labradorius* (Gmel.))! Il en est de même pour la tourte ou pigeon voyageur (*Ectopistes migratorius* (Linn.)), pour le grand pingouin (*Plautus impennis* (Linn.)), etc.!

Nous avons aussi traité des divers aspects d’une signalisation adéquate et uniforme en entomologie pour tous les musées de sciences naturelles et pour les institutions scientifiques ou universitaires qui comptent cette discipline de la zoologie au nombre de leurs richesses actives ou inactives. Le mémoire expose clairement cet important devoir de signalisation non seulement pour les institutions mais aussi pour les entomologistes qu’ils soient ou non intéressés à la systématique.

Nous avons aussi dans cette brochure noté les lacunes de signalisation que les systématistes déplorent vivement et nous avons attiré l’attention des taxonomistes sur l’existence des quelques catalogues que les conservateurs du British Museum of Natural History ont publiés sous le nom de différents auteurs; enfin, nous y suggérons une formule de signalisation uniforme qui semble tenir compte des désiderata et besoins immédiats des systématistes.

C’est avec une légère appréhension cependant que nous avons abordé le problème de localisation et d’accessibilité des spécimens-types éparpillés dans le monde. En ceci, nous différons légèrement d’opinion avec les membres du Comité de l’ICOM dans les suggestions faites sur les termes à employer et sur les mesures à prendre par les dépositaires de matériel type zoologique pour résoudre les divers problèmes d’inaccessibilité.

En fait le Comité de l’ICOM conclut à la quasi impossibilité de remédier à cet état de choses si ce n’est en changeant radicalement certaines règles de la nomenclature de telle sorte que l’établissement d’un nouveau genre ou d’une nouvelle espèce en zoologie soit subordonné au dépot du spécimen-type dans une institution universitaire ou un musée d’envergure nationale. On connaît par le mémoire notre appréciation sur la valeur collaboratrice des musées universitaires en général. Que des savants, particulièrement scrupuleux, se refusent à décrire un spécimen zoologique qui pourrait devenir un type tant que ce matériau appartient à un particulier ou à une petite institution et que sa conservation technique n’est pas définitivement assurée à 100% ne serait pas sans nuire dans une certaine mesure à l’avancement de la science.

On peut très bien avec le Comité de l’ICOM se poser la question s’il ne conviendrait pas de réunir les spécimens-types dans les Musées importants comme les musées nationaux, les musées provinciaux ou d’état ou les musées régionaux vraiment représentatifs. Se poser la question n’est pas y répondre et ne résout pas le problème.

On ne saurait créer aucune voie légale en vue d'ordonner une rédistribution des spécimens-types dans les musées d'une importance donnée et dans les localités les mieux appropriées. Quant à la possibilité d'amener les institutions régionales, locales ou les petits musées mixtes ou de sciences naturelles, tout comme les particuliers d'ailleurs, à s'exécuter de bon gré, c'est là, croyons-nous, un projet qui rencontre trop d'objections à raisons historiques, sentimentales, parfois psychiques et même légales pour nous permettre de l'envisager sous un angle prometteur.

Nonobstant que le spécimen-type est peu ou pas utile au point de vue scientifique dans le petit musée local, il n'est pas sans jeter un certain lustre sur les collections auxquelles il appartient et sur l'institution qui le possède. On peut venir d'assez loin pour le voir et l'examiner mais si l'histoire de ce spécimen-type est attachée à des circonstances flatteuses, intéressantes ou sentimentales, car il y a souvent beaucoup de sentiments dans le petit musée local, cette institution ne voudrait et ne saurait se départir d'un objet que de grands musées tiennent pour précieux sans blesser l'orgueil national ou régional.

Il arrive même que la loi ou les conditions attachées au legs, au don ou à l'achat de collections peuvent s'opposer à la cession d'un tel spécimen-type en faveur d'une autre institution. On sait qu'il s'est déjà trouvé dans un certain musée une collection ornithologique, conservée par un procédé apparemment nouveau et dont la propriété pour le musée intéressé était conditionnelle à une clause de vente qui stipulait qu'aucun spécimen ne pourrait être vendu, cédé, transporté ou prêté sans rendre nul le contrat de vente. La clause comportait même une condition permettant la reprise de la collection par le vendeur sans l'obligation de dédommagement ou remboursement du prix payé.

Après avoir étudié ce problème sous tous ses angles, nous nous sommes efforcés d'y trouver une solution. Celle que nous avons exposée dans le mémoire du Musée de la province de Québec et que nous proposions l'an dernier pour remédier autant que faire se peut au problème d'inacessibilité des spécimens-types nous paraît encore la solution la plus acceptable par tous les dépositaires de matériel type, grands ou petits, peu importe où ils sont localisés. Cette solution évite toute discussion légale, elle respecte le côté historique, sentimental ou psychique sans porter atteinte à l'orgueil régional ou national, au contraire.

C'est évidemment une solution demandant un travail supplémentaire et de longue haleine de la part des dépositaires, travail qui doit nécessairement s'échelonner sur un certain nombre d'années pour être vraiment effectif.

Nous avons clairement défini dans ce petit exposé ce que nous entendons représenter au Musée de la province de Québec par le terme "topohomoeotype" et nous avons strictement délimité l'usage qu'on peut faire de l'objet ainsi désigné. Pour réussir la même combinaison selon les termes que suggèrent le Comité de l'INCOM, il nous faut utiliser le terme topotype déjà admis et le terme proposé de metatype pour remplacer le terme déjà connu d'homoeotype. Nous aurions ainsi, par cette nouvelle combinaison, le nouveau terme de "topometatype" au lieu de "topohomoeotype".

Nous admettons volontiers que les deux termes se valent et sont appelés à rendre les mêmes services; notons cependant que le terme "topohomoeotype" a préséance d'utilisation et que présentant l'avantage d'être la combinaison de termes déjà connus et en usage il aurait mauvaise grâce à céder le pas à un nouveau venu.

Ce petit mémoire contient aussi la suggestion des moyens à prendre pour mettre en branle l'application de cette solution en amorçant un courant d'échanges entre les musées et institutions de sciences naturelles dépositaires de matériel type.

La mise en application d'une telle solution est cependant nécessairement subordonnée à l'acceptation par la Commission internationale de Nomenclature zoologique du terme de topohomoeotype et de la reconnaissance de l'objet ainsi désigné qui, sans appartenir à la catégorie des types primaires en devient un suppléant à rang égal et conséquemment supérieur à tout autre matériel type de rang secondaire.

Puisque la solution proposée rencontre l'approbation de la plupart des entomologistes intéressés à la systématique, il serait peut-être dans l'ordre que cette section du X^{e} Congrès international d'Entomologie exprime le voeu que la Commission Internationale de Nomenclature Zoologique établisse les règles devant servir à la désignation de ce matériel type, qu'elle émette une opinion sur la validation du terme topohomoeotype et qu'elle en sanctionne l'usage en recommandant l'échange de ce genre de spécimens types entre les dépositaires de matériel type entomologique.

Nous sommes d'ailleurs bien convaincus que ce qui peut se faire en entomologie est tout aussi désirable et tout autant possible dans les autres disciplines zoologiques.

DISCUSSION

W. T. M. FORBES. There are two difficulties: 1, topotypes of some species are not available; 2, when specialists are very few, essential material should be in the hands of those specialists.

N.-M. COMEAU. Of course topotypes of some species are not available, but when topotypes are deposited in large museums they are available to all specialists.

Études récentes des Sources de Bibliographie entomologique

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RÉSUMÉ

L'auteur rappelle l'importance des communications de W. Horn aux Congrès Internationaux de Zoologie et d'Entomologie, et, notamment, son exposé au Congrès de Budapest (1929) intitulé: "Über die Not der Entomo-Bibliographie". Cet exposé constitue une remarquable bibliographie de soixante bibliographies entomologiques.

Depuis cette date, les seuls travaux comparables furent ceux de Chamberlin[1]*, Smith*[2]*, et Sawyer*[3] *qui, en dépit de leur grande valeur intrinsèque ne témoignent pas d'une claire méthode bibliographique.*

Tenant compte des progrès très importants de la bibliographie méthodique contemporaine, l'auteur a publié récemment un nouveau guide de bibliographie entomologique, qu'il présente au Congrès[4].

[1] Chamberlin, W. J. 1952. Entomological nomenclature and literature. 3rd edit., W. C. *Brown*, Dubuque, 141 pp.

[2] Smith, R. C. 1952. Guide to the literature of the zoological science. 2nd revis. edit., *Burgess Publ. Co.*, Minneapolis, viii + 133 pp.

[3] Sawyer, F. C. 1955. Books of reference in zoology, chiefly bibliographical. *Journ. of the Soc. for the bibl. of Nat. Hist.* 3 (2): 72–91.

[4] Dupuis, C. 1955. Les sources bibliographiques de l'Entomologiste. *Cahiers des Naturalistes* 10 (Suppl. 1954): 77–112.

L'Importance du Sol dans l'Origine et l'Evolution des Insectes[1]

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ABSTRACT

In solving problems of animal phylogeny, the establishing of environmental conditions in which the given direction of evolution was feasible is of great value. The transition of many invertebrate groups from water to land in the course of phylogeny could take place through the soil, where respiration of air is not associated with desiccation.

The lower representatives of terrestrial groups—Onychophora, Myriapoda, lower insects—are, as a rule, soil dwellers. The phylogenetic series—annelids, myriapods, insects— corresponds with the series of environmental changes—water, soil, air.

The intermediate character of the soil as an environment may be proved by the presence in soil insects of many peculiarities characteristic of aquatic invertebrates (permeability of skin, poikilothermism, orientation by the gradients of dissolved materials, etc.). The theories of primary aquatic habit in insects are of no value in their ecological aspects. The ecologic viewpoint in phylogenetic studies makes it possible to understand the origin of the principal types in the development of the Pterygota. The juvenile stages of primitive insects were inhabitants of the soil, and the adults emerged to the soil surface for mating and dispersal. Evolution took place in two directions. (1) The juvenile stages acquired a mode of life similar to that of the adults and emerged from the eggs in a late stage of development (Hemimetabola). (2) The adults adapted themselves for dispersal, whereas the juveniles retained their retired habits under conditions of good food supply and humidity and hatched at a morphologically earlier stage (Holometabola).

L'étude des particularités du sol comme étant le milieu donne matière à la solution des problèmes cardinaux biologiques, en particulier des problèmes de phylogénie.

Les constructions phylogéniques se basent principalement sur les données des disciplines morphologiques dont la matière a servi de base aux conceptions actuelles de l'évolution. La conception fondée sur cette base: que les groupes d'animaux terrestres proviennent d'ancêtres aquatiques, est une conception généralement admise; néanmoins, les voies de la transition de la vie aquatique à la vie terrestre au cours de la phylogénèse—surtout en ce qui concerne la majorité des groupes des invertébrés—restent jusqu'à présent insuffisamment éclaircies. L'emploi de la méthode d'écologie comparée, l'explication des changements possibles du milieu, l'étude des modifications des organismes dans leur dépendance réciproque vis-à-vis des conditions d'existence peuvent apporter une aide importante lors de la mise au point des voies possibles d'une semblable transition.

Les différences les plus essentielles des conditions d'existence dans l'eau et sur la terre ferme sont: les diverses conditions de la respiration et le danger de périr par dessiccation sur la terre ferme. La quantité de l'oxygène contenue dans l'air est sensiblement plus haute que celle contenue sous forme diluée dans l'eau, mais pour les espèces aquatiques la transition à la respiration de l'oxygène de l'air se complique par le dessèchement des surfaces respiratoires. C'est pourquoi le dessèchement des organes respiratoires est, en premier lieu, le principal obstacle au passage sur la terre ferme des organismes aquatiques.

Le processus même de l'échange des gaz ayant lieu dans les organes de la respiration aquatique—surtout lors de la respiration cutanée—peut se produire également à l'air. Le passage sur la terre ferme des habitants de l'eau aux organes respiratoires aquatiques peu différenciés, respirant surtout par toute la surface du corps, est facile à se représenter comme se réalisant dans le milieu à l'air saturé de vapeurs d'eau dans lequel la respiration par oxygène de l'air est possible avec le minimum de danger de dessiccation.

Pour de nombreux groupes d'invertébrés, un semblable milieu leur assurant la possibilité d'une adaptation progressive vers la respiration à l'air a été probablement le sol dont l'air était habituellement saturé de vapeurs d'eau ainsi que cela a été démontré expérimentalement par A. F. Lebedev déjà en 1911.

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[1] Also published in *Entomologicheskoe Obozrenie* 35 (3): 487–494. 1956. (Russian with English summary.)

D'après leurs particularités physiologiques, beaucoup d'invertébrés vivant dans le sol, typiquement terrestres (sensu latu) respirant à l'air, même ceux qui, comme les larves des taupins se rapprochent des invertébrés aquatiques (sensibilité envers le dessèchement, les propriétés poikilosmiques, orientation d'après le degré de la dilution des matières dans l'eau, la faculté d'user du mode de respiration cutanée, saprophagie, migrations verticales, etc.).

Le sol pris comme milieu d'habitat a beaucoup de points semblables aux milieux aquatiques (contenance élevée de CO_2 par comparaison avec la contenance de l'atmosphère, graduation verticale de la température et ses renversements journaliers et saisonniers, possibilité des migrations verticales et de s'y fixer à n'importe quel horizon, présence de l'eau —phase liquide du système polydisperse à trois phases, etc.).

Beaucoup de pédologues considèrent le fond des bassins comme des sols spécifiques, et les hydrobiologues considèrent l'eau du sol comme étant des bassins spécifiques. Les différences entre le fond des bassins et le sol sont tout-à-fait conventionnelles dans le cas des bassins qui se dessèchent périodiquement, alors que la surface donnée change de caractère selon son aspect saisonnier.

Au point de vue écologique, le sol pris comme milieu dans lequel la respiration par oxygène de l'air est possible sans danger de destruction rapide par dessèchement est un milieu intermédiaire entre le milieu aquatique et un milieu aérien.

Etudions rapidement les représentants des différents groupes d'invertébrés; nous limitons notre étude aux organismes vivants libres (non parasites) dans le milieu aquatique et sur la terre ferme, en distinguant le sol comme étant un milieu indépendant (en y comprenant la litière et les habitats similaires, les cavités en-dessous des pierres, etc. . .). Généralement, ce sont seulement les habitats aquatiques et terrestres qui s'opposent (Hesse, 1924, et d'autres auteurs).

Chez les protozoaires, il n'existe pas de formes véritablement terrestres—tous les protozoaires sont typiquement aquatiques, ou bien ce sont des formes habitant dans le sol. Dans le sol, les Protozoa se trouvent dans les gouttes d'eau du sol ou dans les filmes de l'eau enveloppant les particules solides.

La majorité des Turbellaria sont des formes aquatiques; certains Rhabdocoela et Triclada passent au genre de vie terrestre, alors que pour certains Turbellaria l'habitat même dans le sol et dans la litière est bien caractéristique. Parmi les Nemertini, groupe typique de vers aquatiques, il existe toute une série de forme habitant le sol (Goenemertes). Les nématodes libres habitent dans la mer, les eaux douces et le sol humide, leurs formes marines étant les plus primitives. Parmi les Annelida-Polychaeta, la majorité écrasante revient aux espèces aquatiques-marines or, dans les îles de l'archipel Malais, on a découvert (W. Harms) des polychets terrestres rappelant par leur mode de vie, les caractères des mouvements et par le développement puissant de la cuticule avec les trachées primordiales les myriapodes (*Lycastis vivax*, *Nereis vitabunda* et surtout *Lycastopsis amboinensis*) habitant loin de la mer, ensemble avec les Peripatus et les Myriapoda, tandis qu'en Provence le *Nereis diversicolor* vit à la manière des vers de terre. Parmi les Oligochaeta les "terricoles" sont les formes terrestres, tandis que les plus primitives—les "limicolae" sont pour la plupart des habitants des eaux douces; mais il existe parmi eux des formes terrestres aussi (par exemple les Enchytraeidae). Un exemple intéressant est donné par le Tubifex, typiquement bentique, s'adaptant parfois à la vie dans le sol après l'assèchement du lac surtout. (Harms, 1934).

Parmi les Arthropoda, pour les formes de crustacés, c'est la vie aquatique qui est la plus caractéristique. Cependant, certains auteurs développent une théorie assez paradoxale concernant un retour secondaire des crustacés à la vie aquatique (Simroth, 1891; Foxon, 1935). Chez les Entomostraca, les formes aquatiques prédominent; quelques Harpacticidae seulement se rencontrent dans le sol aussi que par exemple R. Harding a décrit une espèce d'Ostracoda terrestre d'Afrique tropicale. Entre les Malacostraca, c'est chez les Oniscoidea que l'on rencontre les adaptations les plus perfectionnées à la vie terrestre; en les étudiant, on peut suivre toutes les étapes de l'évolution des formes aquatiques vers les formes terrestres. De plus, il existe des représentants des Oniscoïdes habitant même dans les conditions désertiques (*Hemilepistus cristatus* et les autres). Les Isopodes terrestres sont étroitement liés à l'habitation dans le sol et leur connection avec le sol est d'autant plus étroite que le biotope habité par l'espèce donnée est plus xeromorphe. Il y a également des formes terrestres intimement liées au sol et chez les Amphipoda (Orchestia) et chez les Decapoda (Gecarcinidae, Birgus, Coenobita, Cambarus, Engaeus et autres).

Les Onychophora représentent typiquement des animaux respirant à l'air, excessivement sensibles au dessèchement (d'après les expériences de Manton and Ramsay, 1937) et intimement liés au sol. Après la découverte des fossiles de Xenusion et de l'Ayscheya, l'origine des Onychophora à partir des ancêtres aquatique a reçu une preuve paléontologique.

Parmi les espèces d'arthropodes, ce sont les myriapodes et les insectes qui sont les mieux adaptés à la respiration à l'air. Les myriapodes—plus primitives que les insectes, sont des formes typiquement terrestres (s.l.) parmi lesquels il n'y a pas de représentants aquatiques. Les myriapodes inférieurs—les groupes Symphyla et Pauropoda—possèdent un habitat typique dans le sol, dans la litière et des substratums similaires. Chez les Diplopoda, ce sont également les habitants du sol (de la litière) qui prédominent; et ce n'est seulement que dans les forêts humides équatoriales que l'on rencontre des formes habitant à la surface des arbres. Les Chilopoda—groupe se rapprochant le plus, par maints rapports, aux insectes—sont intimement liés au sol; de plus, leur habitat endogé dans le sol est caractéristique pour les Geophilomorpha ayant conservé des caractères plus primitifs. Schizotarsia, le groupe le plus adapté à la vie à surface du sol, est caractérisé par de nombreux traits convergeant vers les insectes (diminution du nombre des segments, leur fusion sans articulation, allongement des extrémités, articulation de la patte, développement des yeux à facettes, etc.).

Pour les groupes inférieurs des insectes, Protura, Campodeidae, Japygidae, la plupart des Collembola et des Thysanura, l'habitat dans le sol et les substratum similaires est typique. Seuls, quelques Apterygota sont aptes à vivre en dehors du sol et sans d'autres abris (Sminthuridae parmi les Collembola). Parmi les Pterrygota, le lien étroit avec le sol et la litière est caractéristique pour des groupes tels que les Blattoidea, Grylloblattoidea. Les liens les plus anciens et les plus solides écologiques des insectes se reflètent dans les lieux de la ponte. Le lien avec le sol est très net chez de nombreux Tettigonoidea et Grylloidea (Stenopelmatus, Schizodactylus). Les Acridoidea sont le groupe le plus affranchi du lien avec le sol parmi les Saltatoria; mais chez eux, les oeufs se développent toujours dans le sol et ne sont pas cleidoïques.

Les Embioidea sont par excellence des habitants du sol. La vie endogée, surtout lors des premiers stades de leur développement, et les liens avec le sol et la litière sont caractéristiques aux Isoptera, qui sont très exigeants quant à l'humidité relativement élevée de l'air.

Parmi les Hemimetabola, ce sont les Rhynchota qui sont les mieux adaptés à la vie à découvert, à toutes les phases du développement. Un lien étroit avec le sol, lors des phases juvéniles du développement, se rencontre chez le Cicadidae, famille considérée comme base du système du sous-ordre des Homoptera.

Dans la sous-classe des Holometabola, le lien avec le sol est également caractéristique pour des formes plus primitives de nombreux ordres. Un lien particulièrement intime avec le sol lors du stade larvaire, alors que c'est le stade imaginal chez les Holometabola—ainsi que chez tous les Pterygota—est toujours plus ou moins adapté à la vie à découvert. Chez les Coléoptères, par exemple, ce sont les stades larvaires des Adephaga et des Polyphaga inférieurs qui habitent principalement le sol. Même chez les familles aussi spécialisées que les Curculionidae, les formes plus primitives se développent dans le sol (Adelognathi, Cleonini parmi Phanerognathi), alors que les Curculionidae-Phanerognathi plus spécialisés se développent dans les tissus, dans les cavités entre les organes de la plante nourricière et même à découvert (Phytonomus). De tels exemples peuvent être cités pour d'autres ordres des Holometabola également.

Les Arachnoidea inférieurs facilement liables aux Xyphosura aquatiques, bien que coutumiers aux localités xerophytes, sont intimement liés au sol (pris dans un large sens) et aux habitats similaires.

La transition des mollusques à la vie terrestre dépend moins de l'utilisation du sol, grâce à la présence des coquilles qui remplissent—chez les formes terrestres—une fonction défensive contre le dessèchement; en cas d'habitat dans le sol où l'air est saturé de vapeurs d'eau, la coquille chez les Gastropodes-Pulmonates se réduit (Testacellidae, Limacidae).

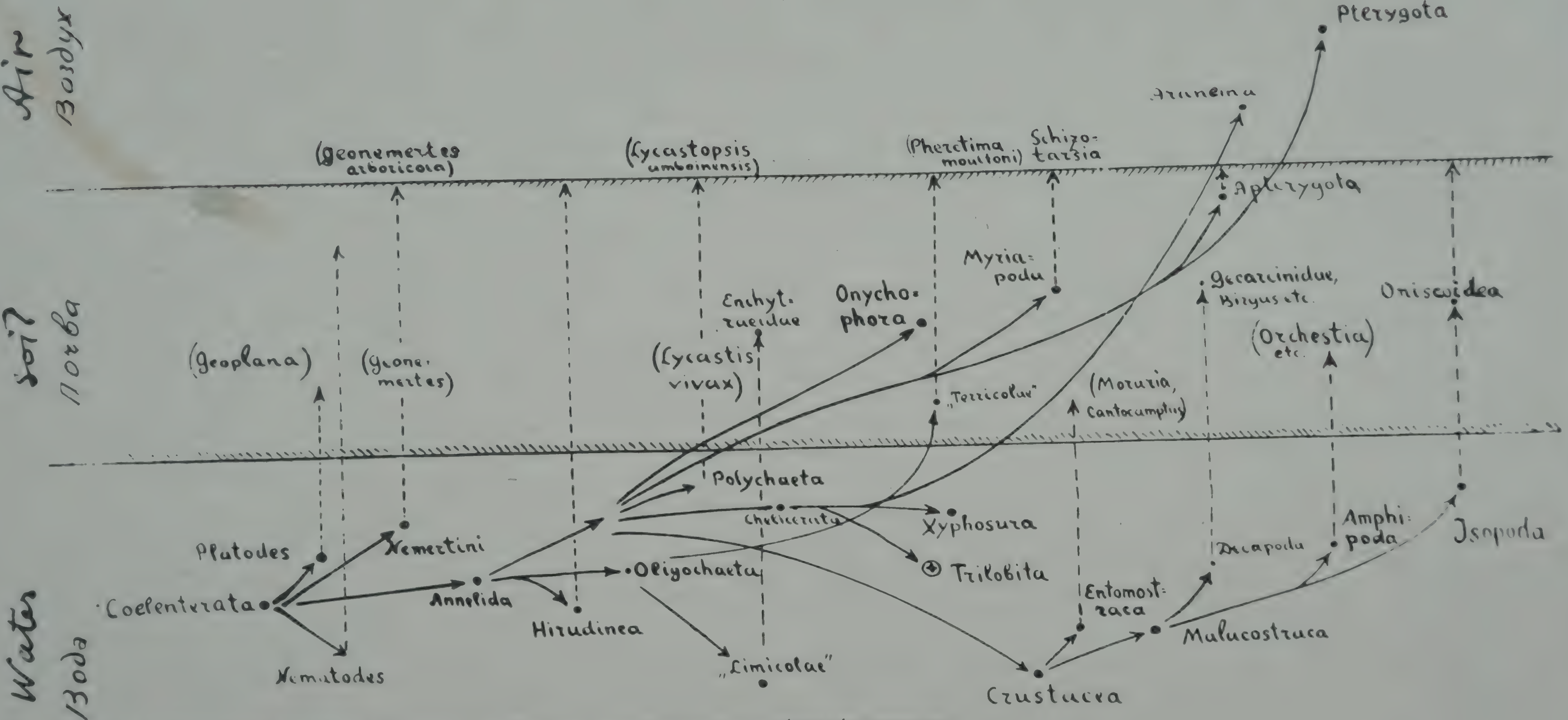
Air
Воздух
Soil?
Почва
Water
Вода
Pterygota
Araneina
(Geonemertes arboricola)
(Lycastopsis umboinensis)
(Pheretima moultoni)
Schizotarsia
Apterygota
Myriapoda
Gecarcinidae, Birgus etc.
Oniscoidea
Enchytraeidae
Onychophora
(Orchestia etc.
(Geoplana)
(Geonemertes)
(Lycastis vivax)
„Terricolae"
(Moraria, Cantocamptus)
Polychaeta
Chelicerata
Xyphosura
Trilobita
Plutodes
Nemertini
Decapoda
Amphipoda
Isopoda
Coelenterata
Annelida
Oligochaeta
Entomostraca
Hirudinea
Malacostraca
Nematodes
„Limicolae"
Crustacea

Fig. 1. Voies écologo-phylogénétiques de l'évolution chez l'embranchement menant aux anthropodes terrestres

Cette brève description des changements de milieux dans le processus d'évolution peut être illustré par un schéma des voies de transition de vie aquatique à vie terrestre. La figure 1 montre le schéma des rapports phylogénétiques probables des plus importants groupes de la branche des Protostomia menant vers les insectes, représentés sous leur aspect écologique; dans ce schéma sont représentés des groupes où il se produit des cas d'abandon du milieu aquatique et de développement en dehors de ce milieu. Les traits pleins représentent les rapports phylogénétiques acceptés par les morphologues (Fedotov, 1924, 1935; Snodgrass, 1938; Størmer, 1944). Les traits en pointillé montrent les voies écologiques dans les cas des transitions du milieu ambiant à un groupe donné vers un milieu ambiant nouveau. Sur ce schéma, le sol est représenté comme milieu ambiant particulier et est compris dans le sens le plus large du terme, y compris la litière et les habitats similaires. Les Pterygota sont montrés par moi comme vivant à l'air, ce qui est juste pour la phase imaginale de la plupart des pterygotes.

Les stades juvéniles, de même que la plupart des Apterygota sont généralement liés à des habitats où le danger de dessiccation est moindre et comme les groupes plus primitifs, sont liés avec le sol.

Si l'on considère le sol comme milieu ambiant particulier (au même titre que l'habitat aquatique et un habitat terrestre à découvert) cela permet de rétablir les conditions écologiques de l'origine des insectes et, conséquemment, de se représenter leur évolution.

Le passage des menus animaux aquatiques du type des annelides, respirant par toute la surface du corps, vers les habitats dans le sol et la litière sert de condition à la formation des caractères des Myriopoda. La possibilité d'une évolution dans cette direction est démontrée par l'exemple des néréides terrestres. Dans les mouvements des animaux allongés et flexibles le long des couloirs étroits, ce sont les extrémités de l'avant-corps qui ont une portée fondamentale. L'oligomérisation, la stabilisation du nombre de segments et la tagmatisation suivi d'adoptation de la partie antérieure du corps à la fonction locomotrice, ont provoqué la formation des caractères distinctifs des Prohexapoda ayant vécu dans les mêmes conditions que les Protomyriapoda qui ont été à leur origine.

L'augmentation de la solidité des téguments (probablement liée primitivement à des fonctions mécaniques) a amené la formation de téguments protégeant l'organisme contre une perte rapide d'eau. La fonction respiratoire passa de la surface entière du corps aux parties spécialisées du corps donnant naissance aux trachées.

Le développement de l'imperméabilité à l'air des téguments a assuré la sortie de ces animaux du sol et de la litière vers la surface. Ces sorties, même en cas de conservation du mode de locomotion propre aux espèces habitant tenier et tunnels (rampement) facilitèrent la dispersion et rencontre des sexes.

En partant des brefs rampements de dispersion, les ancêtres des insectes épigés récents passèrent probablement au locomotion par sauts (ce que l'on peut observer chez de nombreux groupes actuels des Apterygogènes). Un mode de locomotion semblable, compliqué par un transport passif causé par le vent, provoqua un vol sous sa forme primitive, en particulier chez les espèces présentant des excroissances sur le corps. Chez de nombreux Aptèrygotes sensibles au dessèchement, les excroissances dorsales se développent fortement (paranotalia), excroissances dont la fonction première fut toute défensive (Machilis).

L'hypothèse du développement des ailes à partir des excroissances thoraciques paranotales a été développée par Handlirsch, 1925, et la signification des sauts et des "pleurae" chez Machilis pour la compréhension de l'origine du vol a été relevée déjà par Grassi.

L'évolution successive des ancêtres des Pterygota tendait vers l'adaptation du stade imaginal à un type plus parfait de dispersion active vers le vol, vers les habitats épigés.

C'est ainsi qu'on peut se représenter l'évolution des formes primitivement aptères vers les insectes ailés. Avec l'élaboration chez la phase imaginale des adaptations au vol, à l'habitat à la surface du sol, deux voies d'évolutions de l'ontogénèse deviennent probablement possibles. Dans l'un des cas, on peut observer la tendance des stades juvéniles vers des adaptations à un habitat épigé dans les mêmes conditions que les individus imaginaux —voie prise par les Hemimetabola.

Dans l'autre cas, il se présente une tendance vers une divergence des stades différents. A la sortie sur la surface du sol s'adaptait uniquement le stade imaginal apte à dispersion, tandis que les stades juvéniles continuaient à mener un mode de vie endogée, propre aux Protohexapoda. Cette voie est celle des Holometabola.

On peut considérer comme initiale la forme thysanuroïde hexapode pour les stades juvéniles chez les Hemimetabola aussi bien que chez les Holometabola.

La supposition que les ancêtres des insectes habitant et se développant dans le sol et la litière, sous les pierres et dans des endroits similaires caractérisés par un air saturé d'humidité permet de comprendre également les voies qui ont amené l'apparition des groupes d'insectes ayant des larves aquatiques. Les larves habitant auparavant dans le sol et entre les pierres sur les rives, pouvaient facilement passer une seconde fois au mode de vie amphibotique et aquatique. Ainsi, on peut facilement élever des larves des Ephemeroptera à partir de formes proches des Thysanura, dont les formes campodeoïdes juvéniles habitaient sur les rives, entre les pierres. Avec une voie d'évolution parfaitement acceptable au point de vue écologique de la phylogénèse des Ephémeres amphibies (ainsi que des libellules et des Perlides) l'existence du système trachéen chez les larves de ces groupes devient parfaitement compréhensible.

L'acceptation du mode de vie aquatique des larves comme étant initial (Handlirsch, 1925; Laméere, 1922; Martinov, 1938) rend l'apparition du système trachéen injustifiable du point de vue physiologique et écologique. L'apparition des trachées n'est possible qu'en cas de respiration à l'air, quand la respiration cutanée ne peut satisfaire les exigences en échanges gazeux par suite de l'accroissement de la compaticité et imperméabilité des téguments ou de la diminution de la valeur du rapport entre la surface et le volume. Une semblable origine indépendante et convergente des trachées a lieu chez divers groupes d'arthropodes.

L'évolution des stades juvéniles vers une adaptation à l'habitat épigé et sec se rapprochant des conditions d'habitat du stade imaginal mena vers l'embryonnalisation des premiers stades du développement, vers l'hémimetabolie (paurométabolie d'après Berlese et Jezhikov) et vers la nymphalisation des stades juvéniles libre.

L'évolution vers l'adaptation du stade larvaire au mode d'habitat endogé, lors de l'évolution du stade adulte vers l'adaptation au vol, mena vers le maintien des caractères primaires chez les larves et peut-être même vers une éclosion de l'oeuf dans un stade de développement plus précoce (grâce à l'approvisionnement en nourriture) que chez les formes ancestrales.

Cette voie d'évolution—la voie des Holometabola—concorde facilement avec le point de vue de Berlese-Jezhikov sur le caractère embryonnaire de la larve chez ce groupe d'insectes.

Une fois la question ainsi posée, l'infranchissable abîme entre la larve et la nymphe disparaît; c'est de cette absence dont parlent les données de Henson, 1946. D'autre part, la cause de l'imaginalisation de la nymphe devient claire ainsi que son degré d'organisation plus élevé que celui de la larve.

Il résulte d'une telle conception de détermination écologique des deux types de développement que le stade de la chrysalide chez les Holometabola se développe indépendamment mais, que d'après le niveau morphologique général, il est de même comparable au stade des nymphes chez les insectes à métamorphose incomplète.

C'est ainsi que l'hypothèse des voies de l'évolution écologique des insectes exposées ici concorde avec la conception phylogénétique et physiologique de Kozhantchikov (1946) et avec les thèses fondamentales de Berlese (1913) qui, à première vue, sont opposées l'une à l'autre. L'existence d'un nombre, approximativement le même, d'âges chez les nymphes des insectes à métamorphose incomplète et des insectes larvaires à métamorphose complète, ne reflète probablement rien que les conditions de croissance dans leurs règles générales en présence de téguments sclérotisés compacts.

Les insectes volants primaires ("Protopterygota") passèrent leurs stades juvéniles campodéoformes dans le sol ou dans des substratum similaires et c'est seulement dans leur phase adulte (en principe morphologiquement similaire) qu'ils sortirent à la surface pour l'accouplement et la propagation. L'évolution suivante chez les "Protopterygota" prenait deux directions. Chez les uns on remarquait la tendance vers une ressemblance du mode de vie des larves et des insectes parfaits. Chez eux, l'évolution tendait vers l'éclosion d'une larve plus volumineuse et vers la ressemblance du mode de vie de la larve du stade adulte. C'est la voie des Hemimetabola.

Le renforcement de la lutte pour l'existence parmi les "Protohemimetabola" a produit une divergence des stades imaginaux adaptés à l'habitat épigé et a entraîné la radiation écologique des stades juvéniles ayant—dans beaucoup de cas—perdu leur liaison avec le sol et abandonné le mode de vie endogée.

Aux étapes précoces des "Protohemimetabola", en partant des formes ayant leur habitat dans le sol des rives et sous les cailloux, des embranchements se détachèrent, dont les stades juvéniles sont passés (secondairement) au mode de vie aquatique et ont donné naissance aux Ephemeroptera, Plecoptera et Odonata contemporains.

Un exemple d'un tel passage, observé de nos jours, est donné par la larve des Osmylus chrysops. Cette larve thysanuroïde vit entre les pierres aux abords de l'eau ou dans l'eau mais est dépourvue de branchies et respire au moyen d'une paire de stigmates et par toute la surface du corps.

L'embranchement des "Protohemimetabola" qui continua à mener, dans ses grandes lignes, une vie endogée a donné naissance à des groupes tels que les Isoptera, les Embioptera et probablement les Psocoptera et les Zoraptera.

La direction prise par la plupart des embranchements des Hemimetabola est le passage à un mode de vie épigée et à la phytophagie—qui est encore peu prononcée chez les Blattoidea et chez les Dermaptera, plus prononcée chez les groupes des Orthoptera et qui atteint sa plus nette expression chez les Rhynchota. Pour ces formes, le rapprochement du mode de vie épigée des phases imaginales est caractéristique; rapprochement qui est lié avec l'habitat dans des conditions où l'humidité est insuffisante et amenant l'embryonnalisation des premiers stades, suivie de l'augmentation dans l'oeuf des réserves vitelliques et de l'éclosion d'une phase plus différenciée (la nymphe).

L'organisation générale des naïades, tout en excluant les caractères de l'adaptation au milieu aquatique, est plus proche de l'organisation des Protopterygota primitives, se développant dans le sol que des nymphes des Orthoptera, par exemple, ou des Rhynchota.

Une autre direction prise par l'évolution des Protopterygota mena vers une divergence des phases: la phase larvaire avec fonction nutritive et continuant à mener un mode de vie endogé et la phase imaginale avec fonction de propagation et passage à la vie épigée. L'adaptation des phases juvéniles et adultes aux différents modes de vie créa la nécessité d'élaborer un stade intermédiaire, le "stade de réorganisation"—c'est la phase de la chrysalide.

Le fait de se trouver dans des substratum pourvus de matières alimentaires, a conduit les larves à une éclosion à des stades plus précoces de différenciation morphologique que chez les Hemimetabola.

Ce sont les larves campodeiformes possédant des cercaes (larves oligapodes, d'après la terminologie de Berlese-Jezhikov-Imms) caractéristiques pour les groupes inférieurs des coléoptères qui s'écartent le moins des formes juvéniles des Protohexapoda. Partant de ce type de larves, on peut se représenter des larves apodes ou bien des larves spécialisées.

L'augmentation de la production des oeufs et l'éclosion des larves à un stade encore plus précoce (liée à l'assurance de l'approvisionnement de la larve) ont pu conduire à la formation des larves polypodes pourvues de pseudo-pattes se développant aux endroits de la naissance des extrémités embryonnaires.

L'évolution des phases imaginales vers une adaptation au mode de vie épigé est caractéristique pour différentes branches de Holometabola et peut être observée et dans l'ordre des coléoptères, et dans le complexe des neuroptèroides et dans le complexe des heminopteroides et dans les embranchements des Mecoptera-Diptera et des Trichoptera-Lepidoptera. L'évolution se développe dans le sens de l'adaptation à une activité diurne, c'est-à-dire vers une moindre dépendance envers le facteur d'humidité, vers le métabolisme plus actif.

Les stades larvaires des familles supérieures dans des ordres différents, se sont également adaptés à un mode de vie épigée et on observe chez de nombreux groupes un retour secondaire à la vie aquatique—surtout chez les plus primitives familles.

La figure 2 représente schématiquement la substitution de milieu pendant l'évolution chez les principaux ordres d'insectes.

Je considère comme milieu ambiant principal celui où s'écoulent les stades juvéniles, tout en tenant compte du fait que l'on peut regarder les stades imaginaux des Pterygota comme étant adaptés à la vie à l'air. Dans le cas des Hemimetabola, le rapport entre les conditions de vie des stades des nymphes et celles des insectes parfaits est plus étroit; il donne un rapport plus net de la caractéristique écologique de l'espèce que dans le cas des Holometabola dont les phases imaginales et larvaires sont adaptées aux différentes conditions du milieu ambiant et parfois entrent même dans différentes biocénoses.

C'est pourquoi je fais dévier un embranchement séparé pour les Holometabola (Fig. 2). Dans mon schéma, le départ de la même souche de tous les Holometabola et leur opposition aux Hemimetabola n'ont qu'un sens tout euristique, schématique. Une transformation complète pouvait surgir et indépendamment chez les différents embranchements des Pterygota; mais il n'entre pas dans le domaine de mon exposé d'établir les liaisons phylogénétiques entre les différents ordres d'insectes.

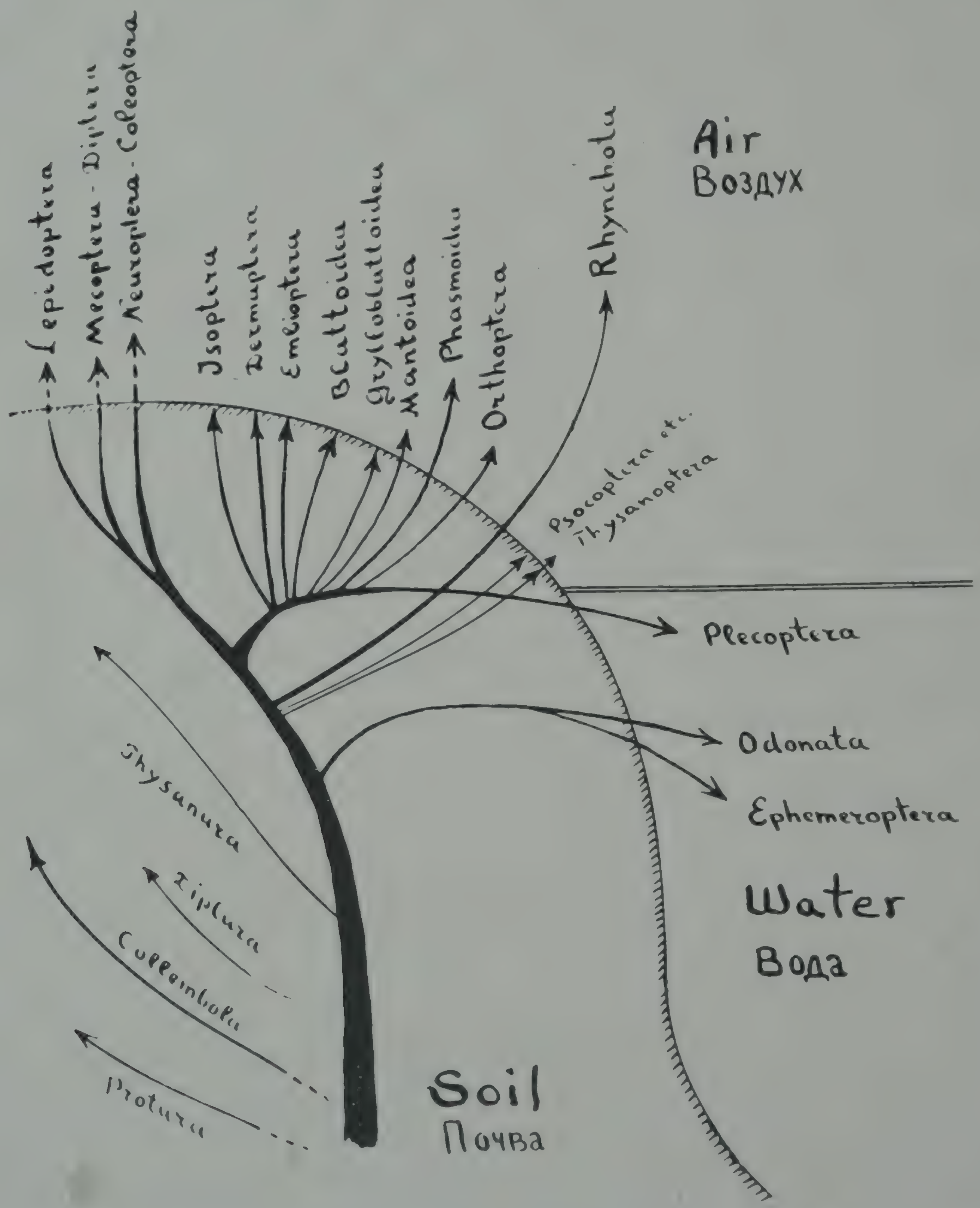
Lepidoptera
Mecoptera - Diptera
Neuroptera - Coleoptera
Isoptera
Dermaptera
Embioptera
Blattoidea
Grylloblattoidea
Mantoidea
Phasmoidea
Orthoptera
Rhynchota
Air
Воздух
Psocoptera etc.
Thysanoptera
Plecoptera
Odonata
Ephemeroptera
Thysanura
Diplura
Collembola
Protura
Water
Вода
Soil
Почва

Fig. 2. Voies écologo-phylogénétiques de l'évolution chez les insectes.

Les données citées démontrent que la mise en évidence du sol (et des substratum ressemblants par leurs propriétés physiques) en qualité de milieu spécifique et l'opposition de ce milieu aussi bien qu'à la terre ferme et qu'à milieu aquatique, ainsi que l'analyse des conditions de l'existence dans le sol, donnent la possibilité de poser des fondements écologiques sous les édifices phylogénétiques bâtis au moyen de matériaux morphologiques.

L'absence presque absolue des formes transitoires entre les groupes d'invertébrés aquatiques et les groupes d'invertébrés terrestres en état fossile s'explique par le fait que l'habitat de ces formes dans le sol rend insignifiante la possibilité de leur conservation étant donné que c'est dans le sol que se passent, de la façon la plus complète, la décomposition des restes des matières organiques, leur minéralisation et leur transformation en humus amorphe.

Ceci limite les possibilités de faire appel aux données paléontologiques dans la solution des problèmes ayant trait à la provenance des myriopodes et des insectes.

DISCUSSION

K. CHRISTIANSEN. As true soil forms usually show some degree of specialization, is it not probable that the plant litter represents the true transition from the aquatic to the epigeous way of life?

M. S. GHILAROV. We regard the litter as the upper layer of the soil. It is impossible to find a true borderline between litter and soil, and the animals migrate up and down. Burrowing forms are, of course, secondary and specialized.

H. H. ROSS. Regarding plant litter, it is now believed by many geologists that plants existed in greater abundance and at an earlier age than was formerly believed. Is not your phylogenetic reconstruction a substantiation of this belief?

M. S. GHILAROV. Yes. It is probable that soil and duff insects occurred in the Precambrian.

The Origins and Growth of the Department of Entomology of the British Museum

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ABSTRACT

Although the entomological collections of the British Museum were only formed into a separate department as recently as 1913, their history goes back to the earliest days of the Museum, which was created in 1753 under the terms of the will of the distinguished naturalist and physician, Sir Hans Sloane. Reference will be made to some of the entomological collections which formed part of this original foundation, to their fate, and to some of the men who had charge of them. The growth of these collections during the 200 years that have since elapsed will be traced in outline, and some account is also given of the expansion of staff, of storage problems, and of the extent of the present collections.

Like most ancient institutions in Great Britain, the Department of Entomology of the British Museum (Natural History) was not created at a stroke. Its roots lie buried deep in the past, and are now so remote that almost all trace of them has been lost. Yet a certain number of facts are on record, and some of the very earliest collections remain.

It is to Sir Hans Sloane, physician to George II, that we owe these early collections and, indeed, the very foundation of the British Museum. He had throughout his life assiduously collected all manner of 'rare and curious things', and at his death in January, 1753, offered the whole of this to the nation for the sum of £20,000, "that it might be preserved and maintained, not only for the inspection and entertainment of the learned and the curious, but for the general use and benefit of the public to all posterity".

It is recorded that when these proposals were submitted to George II, he dismissed them with the remark: "I don't think there are £20,000 in the Treasury". Fortunately the country was not entirely devoid of far-sighted men, and eventually a public lottery was organized to raise the money needed and in other ways to give effect to the Act of Parliament of 1753 which created the British Museum; 100,000 shares in this lottery were issued at £3.0.0d. each. All were sold in six hours, for two-thirds of the money was offered in prizes, the remaining £100,000 being considered ample for the purchase of the Sloane and other collections, for the purchase of a repository for these collections, and also for the provision of an annual income. It is interesting to note that the annual provision now-a-days for the British Museum (N.H.) is something like £750,000. Incidentally, the lottery to which we owe the British Museum gave rise to a great public scandal. A certain racketeer seems to have contrived more or less to corner the market, re-sold the tickets at a premium, and brought many families to ruin. However, the money was raised, the collections were saved, Montagu House, Bloomsbury, was bought, and the British Museum was created.

Of the entomological content of the original British Museum no precise record has survived, assuming that one ever existed. All that has come down to us from that date is contained in the Petiver collection, and, somewhat curiously, in the Sloane Herbarium. It is recorded that in 1725 the Sloane Museum contained in the Linnean sense 3,824 insects. At the time of his death this number had increased to 5,439. Of these, the only specimens that can certainly be recognised are the insects contained in the Plukenet, Petiver, and Buddle collections.

Leonard Plukenet (1642–1706) was a distinguished botanist; his herbarium included a bound volume of 104 pages, on most of which insects were pressed like flowers, though sometimes glued. In this volume there still remain some 1300 recognisable British insects, representative of all orders and in good systematic arrangement.

Of James Petiver (1658–1718) it is said that, through his acquaintance with seafaring men, he procured a greater quantity of rarities and curios than any man before him, indeed too many for this purse, so that they passed eventually to Sir Hans Sloane for £4000. Among them was a collection of insects contained in small glass boxes, and another in which the specimens are flattened between two sheets of mica, which in turn are fixed by gummed hinges to the pages of two large folio volumes. Unfortunately very many have been lost, but there still remain some 850 recognisable specimens, many of them individually listed in Petiver's *Gazophylacium*.

Of Adam Buddle (c. 1660–c. 1715) nothing is known as an entomologist. Nevertheless two of the volumes of his collection of plants, which is contained in the Sloane Herbarium, have about 150 recognisable British and some foreign insects pressed amongst the plants. Amongst them are *Aporia crataegi*, *Melitaea cinxia* and even two wings of an *Argynnis lathonia*. Many of these specimens also carry references to Petiver's *Gazophylacium*.

Thus we see that of the 5,439 "insects" in the original British Museum, we can now only locate with certainty some 2,300 specimens, and the bulk of these are not in the Entomological, but in the Botanical Department and, therefore, may in fact never have been included in the original total. That there were other insects is evident from the privately published *Synopsis of the Contents of the British Museum*. It is recorded there, for example, in the second edition, published in 1809, that on 'Tables 1 and 2 (in Room X) was deposited Sir Hans Sloane's Collection of Insects'. Apologetically, the author goes on to say 'considering the length of time since this collection was formed, and the perishable nature of articles of this kind, it will not appear extraordinary that this part of the Museum should be inferior to the rest in point of preservation'. This statement seems to provide the clue to the fate of those earliest specimens; probably they were destroyed by *Anthrenus*. Nevertheless there were still extant at that time 'the great Hercules beetle', the elephant beetle, golden beetles, the walking leaf, the great lanthorn fly, locusts, butterflies, moths, dragon flies, bees, wasps, etc. There were also other 'more select specimens' preserved elsewhere in one large and four small cabinets, stored thus to avoid further injury from constant exposure to the light. It is doubtful whether any of these still exist, or whether the light was the real cause of the trouble.

Having got away to a somewhat difficult start, the Museum seems to have relapsed into a state of quiescence which lasted until early in the nineteenth century. With Parliament beginning then to take a greater interest in the upbringing of its child than it did in its birth, things began to 'look up'.

The appointment of Dr. W. E. Leach in 1813 marks quite definitely the re-awakening of entomology in the Museum. Leach organised the first 'general collection of insects', i.e., a systematic collection such as has been maintained ever since; he corresponded widely with continental entomologists of his time; published many papers, and bought and exchanged material widely, but after only nine years' service he resigned his appointment in 1822.

In 1821, George Samouelle was appointed assistant to Dr. Leach, and it is to him we owe all that is known of the events of the next twenty years. He is best known as the author of the *Entomologist's Useful Compendium* (1819), a work in some ways ahead of its time and said to have been based, in fact, almost entirely upon the manuscripts of Leach. Certainly Samouelle's later work fell far short of this early promise. However, he was a good curator and kept voluminous notes. Those that survived him form three bound volumes preserved in the Department. From these we learn that, in 1821, 3,565 species were represented in the British collections. By 1836 this figure had grown to 6,176 species represented by 21,296 specimens (*Ent. Memo.* 3: 220 and 2: 100). A census prepared then shows a total of 72,813 specimens. All the available internal evidence tends to indicate that practically all this large increase was due to the activities of Leach and Samouelle. Samouelle's numerous memoranda show that he had a keen interest in his work, and in the furtherance of entomology. He even encouraged visitors, a grave offence through which he incurred the displeasure of the Trustees. A minute, dated January the 18th, 1840, records that:—

> 'Mr. Samouelle having stated in his report of the 8th January that he "had attended nine students to name their insects". . . . the Trustees . . . ordered that neither Mr. Samouelle nor any other Assistant . . . shall in future be interrupted in their duties by such employment; and further order that no person shall henceforth be allowed to bring specimens for the purpose of naming them. . . .'

However, he suffered a variety of setbacks in health and in his finances, and soon after receiving the Minute just referred to, his services were dispensed with. It is not improbable that some of us now-a-days having responsibilities for the entomological collections in the Museum would at times rather welcome an instruction such as that given to the gentlemen of the Natural History Department in 1840.

In 1835 Adam White was appointed. He appears to have been a man of immense industry who set himself the almost impossible task of 'cataloguing every individual specimen in the insect collections; it is perhaps not altogether surprising that he eventually retired suffering from "mental indisposition", a fate that overtook not a few others in the years to follow. As a monument to his industry there remain some forty volumes of manuscript catalogues, every one of which carries his handwriting.

For some sixty years or more after the foundation of the British Museum no attempt whatever was made to catalogue the entomological collections. The acquisition of Dr. Leach's collection in 1826, however, seems to have called somebody's attention to the desirability of instituting some kind of Register. A dual system was initiated. First every specimen was entered as received, and given a number. Secondly, every species was given a number, and the specimens entered again under the species number. This manuscript catalogue is often referred to by Samouelle as the "General Catalogue of the Museum", and his notes fix the date of its inception as about 1828. The system was cumbersome and, due to the fact that a high proportion of the specimens received were unindentified, to say nothing of their gross numbers, was bound to break down before long. It was abandoned, in so far as the serial registration of individual specimens was concerned, in September, 1840. The species register lasted another twenty years. Registration as now practiced started in 1838 in respect of insects, and ever since then only collections, not specimens, have been registered. The number of collections registered to date totals 29,153, varying in size from one insect to 750,000 in the case of the Oberthur Collection, and some 2,500,000 in the Rothschild Bequest, the largest single acquisition ever received.

In 1837 a "Zoological Branch" of the Natural History Department had been formed, and J. G. Children was placed in charge. Children's output as an entomologist was not great; his chief claim to be remembered is that it was in his rooms in the Museum that the Entomological Society of London, of which he was the first president, was born. In 1840 he was succeeded by J. E. Gray, a man of a very different kind. Shortly after his appointment the present British Museum building at Bloomsbury was erected, and the collections moved into the Insect Room. During Gray's tenure of office, the irregularly published and rather scrappy annual *Lists of Additions to the British Museum* were replaced by *Catalogues* and *Lists* of the Collections. Between 1844 and 1866 some eighty of these small volumes were published, varying greatly in scope and merit. Some were bare enumerations of specimens, many of them still unnamed; some were synonymic lists; some were descriptive catalogues. The small staff available was unable to cope with the task, imposed on it from above, of cataloguing and listing not only all the insects in the Museum, but all the known insects, and Gray enlisted the help of temporary assistants. The result in one respect was disastrous, for one of these temporary assistants was Francis Walker.

Of Francis Walker it is said that he was paid on the basis of so much per species described (though the records do not confirm this), with results that are all too familiar to entomologists. If, while he was at lunch, somebody altered the position of his mark in the box he was working at, he was liable to describe again as new after lunch the species he had already described as new before lunch. In this way single specimens are known to have become the type specimen of three different Walkerian species. The fierce criticism aimed at Walker would with greater justification have been levelled at the authorities who encouraged such monstrous practices, rather than against the amiable old gentleman who performed them.

With the retirement of Gray in 1874, and the appointment of Dr. Günther, we begin to enter the modern era, and a far more scientific atmosphere started to spread through the Museum. By this time the collection already contained something like 750,000 specimens, and shortly afterwards, about 1882, these were moved into the present Natural History Museum at South Kensington, where they were allotted space in the S. W. Basement. The hymenopterist, F. Smith, had retired, and A. G. Butler, Charles Waterhouse and W. F. Kirby had all been appointed. They were amongst the last of the 'characters' of the

Museum. Butler spent a lifetime describing butterflies, though his heart was in the Bird Room; Kirby was always terrified lest one should disturb the ever-present "little people" in which he firmly believed, and my chief recollection of Waterhouse was of his frock coat and the silk hat which he always put on whenever he left his room, even to go to the room next door. Kirby's admirable synonymic catalogues are well known and still used. Waterhouse's publications were concerned almost exclusively with the Coleoptera; but it is probably known to few now that the arrangement of the Insect Gallery, including the dissections and the guide, were almost entirely his work. A very great part of it remains still just as he left it.

With the turn of the century a realisation of the importance of insects had penetrated even into the fastnesses of governmental circles, mainly owing to the discovery of their disease-carrying habits. Staffs were increased accordingly, though not adequately, and the "Insect Room" gradually expanded till it occupied the whole of the South West Basement and became, in 1913, a separate Department of Entomology. Even the eleven full-time entomologists, who then formed the staff of the Insect Section, were inadequate to deal with the flood of overseas inquiries, and it was left to private enterprise (the Bureau, now the Commonwealth Institute, of Entomology) to attempt to remedy official shortcomings. Even now, however, with about a hundred persons working daily in the Department, which has been housed in a new building specially erected for it, it is no nearer achieving a complete systematic survey of the insect world.

A history of Entomology in the British Museum, were it possible to write one, would be a history of entomology. There have, until comparatively recently, been very few advances made in systematic entomology to which the Department has not contributed; and it has been fortunate that it has been able, as it were, both in time and space, to march hand in hand and to keep in step with the development of the science on a world wide basis. The first insects to come from America are there; many of the first specimens from the East, from Australia and New Zealand, and a very high proportion of the earliest African insects have found safe deposit there.

I have attempted to sketch the growth of the collections, and of some of the personalities involved, over a period of some two hundred years from a few neglected curios to the most valuable and considerable collection of its kind in existence, numbering well over fifteen million specimens, tended by a permanent staff of more than sixty, and exceedingly rich in historical, and type specimens — a great asset, but also a heavy liability, for the staff conceive it their duty not only to conserve this asset, but also to make freely available to all the information to be obtained from it.

El Raro Cariotipo *Dichroplus silveiraguidoi* Liebermann y la Conveniencia de la Colaboracion Entre Entomologos y Citologos

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ABSTRACT

This work was started because of doubts of the taxonomy of certain specimens of Acridoidea *(Orth.) of Uruguay. This fact was particularly evident in the case of* Dichroplus pratensis *Bruner as compared with* D. silveiraguidoi *Lieb. and that of the former one with* D. pratensis (?). *All these cases were studied both from the morphological and cytological viewpoint and the conclusion reached was that* D. pratensis *and* D. silveiraguidoi *are two definitely different species.* D. pratensis *Bruner and* D. pratensis (?) *have small morphological differences but are cariologically different.*

The case of Scyllinops bruneri *(Rehn) and* S. pallida *(Bruner) which apparently belong to a single species was also studied. On the other hand,* Dichroplus conspersus *Bruner and* D. conspersus ferruginosa *should be separated as they are cytologically different.*

In this work the problem of classification of insects is solved by the close collaboration between entomologists and cytologists. The authors base their study on the concepts and definition of species given by White (1951), Hurst (1933), Stebbins (1950), and Saes (1956a).

A table with cytological data on 32 Uruguayan species of Acridoidea *is presented.*

The population of D. silveiraguidoi *Lieb. is established in accordance with modern concepts of evolutionary cytology.*

INTRODUCCION

Este trabajo es fruto de la colaboración entre la Facultad de Agronomía, el Departamento de Citogenética del Instituto de Investigación de Ciencias Biológicas y la Oficina Nacional del Servicio de Lucha Contra la Langosta (Ministerio de Ganadería y Agricultura).

Se desea expresar reconocimiento hacia el Jefe del referido Departamento, Dr. Francisco A. Saez, y a nuestro compañero D. Enrique Valdes, por—sus aportes que han hecho posible la realización de este escrito.

CONSIDERACIONES GENERALES

En entomología, con una relativa frecuencia, ocurren dudas para separar individuos de distintas especies y hacerlo en forma segura; igualmente, a veces, se tienen dos insectos clasificados separadamente cuando en realidad pertenecen a la misma especie.

Por esta razón consideramos que existen, con criterio amplio y desde varios puntos de vista, al menos aparentemente, en el terreno taxonomico, dos caminos, por un lado el de los individuos dispuestos por los cito-taxónomos, que se encontraría más capacitado para diferenciar especies aún dentro de una especie del morfo-taxónomo, según lo expondremos más adelante. Es así que podría ocurrir, ademas que lo que el morfotaxónomo considera como dos o más especies, no se trate más que de una (hecho ocurrido frecuentemente en entomología). Por esta razón se ubicaría el cito-taxónomo en un lugar, al menos, de— aparente superioridad.

Por todo ello es muy importante para nuestro sentir todo lo que se diga acerca de la especie y sus problemas. White (1951) sobre esto, dice:— "El hecho de que haya un "problema de las especies" no quiere decir que éstas no son entidades perfectamente reales y naturales; significa meramente que los taxónomos no concuerdan a veces acerca de la clasificación (rotulación) de los especímenes de museo y que las "especies" así creadas son algunas veces artificiales. Pero esta artificialidad (allí donde existe) no es inherente al material; sino al fracaso muy humano, de los taxónomos, o al reducido número de especímenes utilizados, o al hecho de que la mayoría de las nuevas especies están descriptas sobre unos pocos carácteres morfológicos sin estudio biométrico, ecológico o zoogeográfico".

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A los motivos expuestos y otros que plantearemos se debió nuestra necesidad de acudir al citólogo para disipar las dudas sobre si las actuales especies de acridinos *Scyllinops bruneri* (Rehn) y *Scyllinops pallida* (Bruner) son tales o no son más que una. Estas dudas se basan, entre otras cosas, en la similitud de la morfometría externa y en la frecuencia con que encontramos en el campo individuos macho y hembra de una y otra especie copulando. Además de la observación del numeros o material de *S. bruneri* y *S. pallida* de nuestra colección, tenemos desde los individuos aparentemente bien definidos de la especie *S. pallida* y los de *S. bruneri* toda una gradación de ejemplares intermedios, que indicarían inter cruzamientos o que estamos ante la presencia de una sola especie.

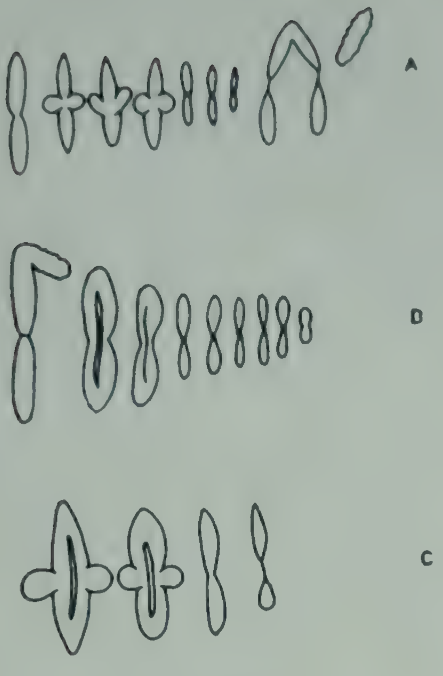
Por otro lado tenemos individuos determinados como pertenecientes a la especie *D. conspersus* Bruner por J. Liebermann, que difiere cromáticamente y morfologicamente con la *D. conspersus* Br. típica. La especie *D. conspersus*, ferruginosa (la primera de las citadas) habita en las cimas de las sierras (zonas predominantemente pedregosas, graníticas o basalticas) con vegetación rala, baja y arbustiva, mientras que la *D. conspersus* típica habita praderas de vegetación graminasea y relativamente alta (no arbustiva) y más rica en agua. Es aquí donde aparece otra duda que aspiramos sea disipada por el citólogo.

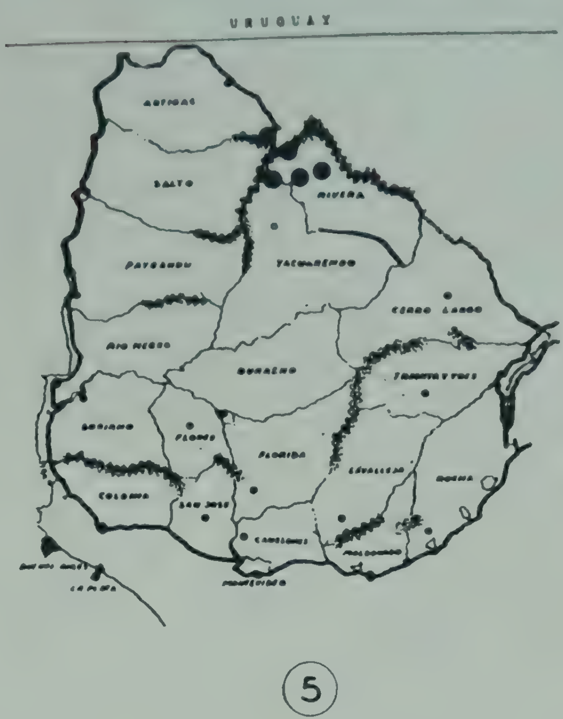
Un hecho similar a este último caso ocurre con la especie *Dichroplus pratensis* (Bruner) y los individuos que calificaremos como *D. pratensis*(?). En estos las diferencias morfologicas son muy mínimas.

En la comparación de las morfologías externas de lo que llamamos *Dichroplus pratensis* (?) y su forma más similar *Dichroplus pratensis* Bruner, tenemos:

	MACHOS	
	D. pratensis (?)	D. pratensis Bruner
Fúrculas	Cuadrangulares, pequeñas y cortas.	Digitiformes, largas y finas.
Cercus	Finos y agudos, como triángulo isósceles.	Más gruesos y sub espatuliformes.
Apéndice prosternal	Iguales.	Iguales.
Pronoto, vista dorsal.	Rectangular.	Trapezoidal, divergiendo hacia la cauda.
Pronoto, vista de lado.	Similár.	Similár.
Longitud total, promedio.	– – –	1/10 mayor que la cotejada.
Robustez	Menos robusta, en general que la cotejada.	– – –
Coloración general.	En general más débil que la cotejada.	– – –
Coloración pronoto.	Castaño en toda su área dorsal.	Castaño oscuro en zona centro con dos bandas laterales divergentes amarillentas a los lados.–

Citologicamente Saez ha demostrado que están caracterizadas por cariotipos distintos, tal como puede verse en la Fig. 4. Cabe destacar en este orden de hechos que *D. pratensis* Bruner por su constitución cromosómica puede producir hasta 4 gametos masculinos diferentes y dos gametos femeninos distintos lo cual significaría la presencia de ocho tipos diferentes de individuos que podrían hallarse en la naturaleza.

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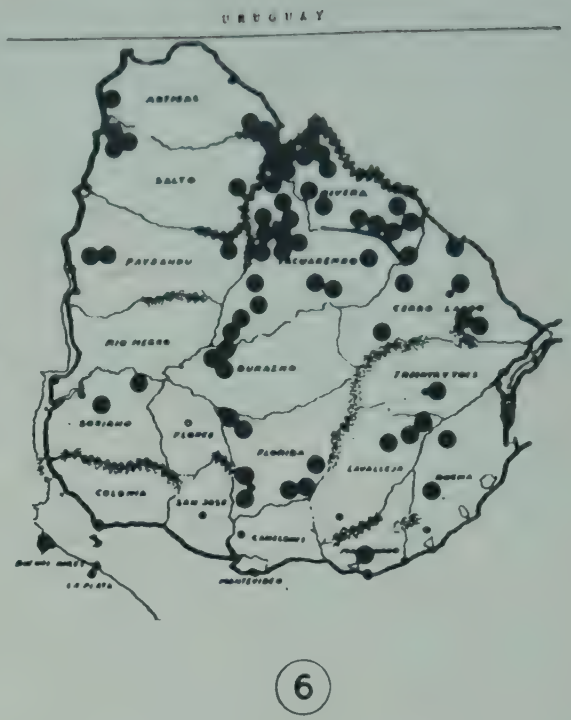
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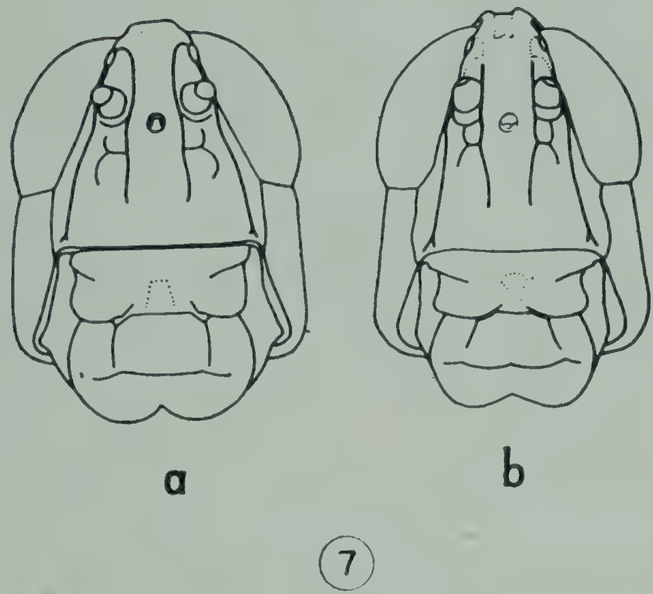

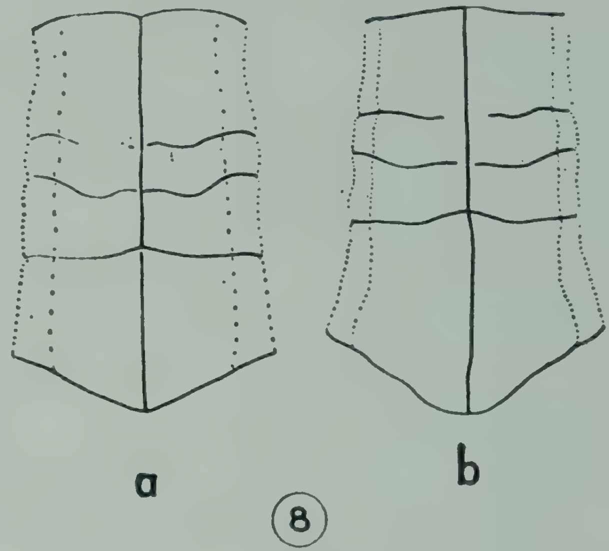

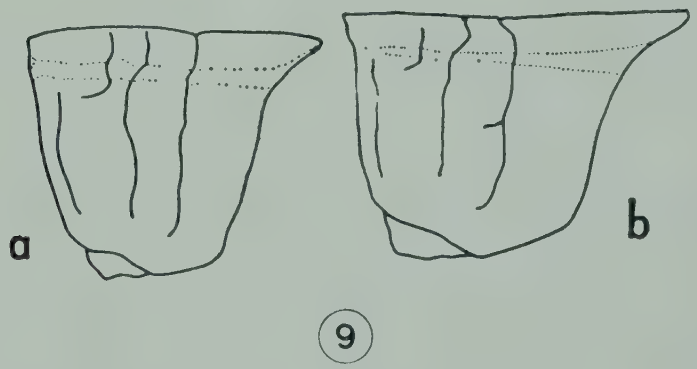

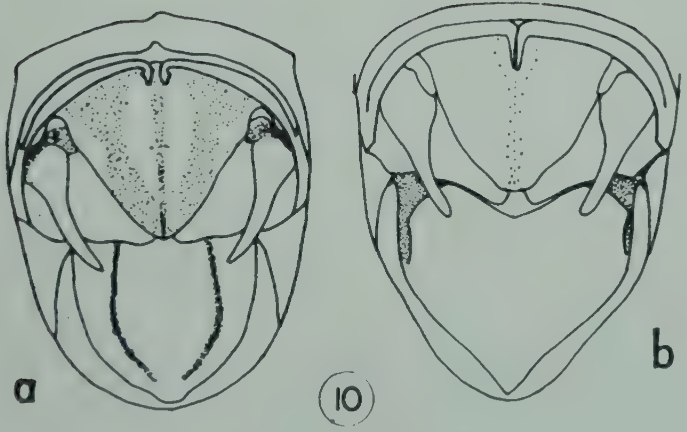

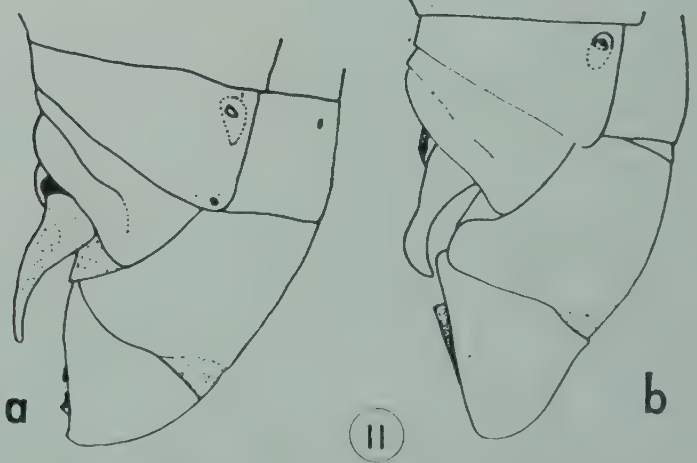

Fig. 4. Representación del cariotipo de *Dichroplus* spp. (A), *pratensis* Bruner; (B), *pratensis* (?); (C), *silveiraguidoi.*

Figs. 5–6. Distributión geográfica de *Dichroplus* spp. 5, *silveiraguidoi.* 6, *pratensis.*

Figs. 7–11. (A), *silveiraguidoi* y (B), *pratensis.* 7, Vista frontal de las cabezas. 8, Vista dorsal del pronoto. 9, Vista lateral del pronoto. 10, Vista dorsal de los segmentos abdominales (IX, X, XI). 11, Vista lateral de los segmentos abdominales (IX, X, XI).

Veamos, la comparación citológica:

Especie	Número diploide de 2n(♂)	Número de metacentricos	Cromosoma X	Número de brazos, cromosómicos
Dichroplus pratensis Bruner.	18	1	Libre	19
Dichroplus pratensis (?)	18	5	Unido	23

Con respecto a *Dichroplus silveiraguidoi*, principal objeto de este trabajo (Liebermann 1957), quien describe la especie que descubriéramos, nos escribe: "Se trata de una especie morfológica y cromaticamente parecida a *Dichroplus pratensis* Bruner, pero braquiptera; asimismo llama la atención el tamaño menor, especialmente en el macho, pues la hembra tiene el aspecto de una hembra de *D. pratensis* Bruner con alas cortas. Hay, sin embargo antecedentes sobre variaciones de tamaño y de longitud de alas en acridios que no se toman como caracteres específicos (J. A. Rehn, 1938) y nosotros hemos mencionado en uno de nuestros trabajos sobre acridios patagónicos (J. Liebermann, 1951) formas reducidas de *Dichroplus pratensis*, aunque siempre macropteras".

"Rehn, en un interesante trabajo (J. A. G. Rehn, 1938) sobre el macropterismo y braquipterismo en *Dendrotettix quercus*, al poner en evidencia que *D. longipennis* Pack no era más que la fase macroptera de *D. quercus*, señala la longitud alar como una simple variación morfológica debida a las condiciones de vida de la especie y según su ubicación dentro de su área geográfica. Para este autor el dimorfismo alar sería resultado de la economía biológica de la especie".

Hasta aquí el Dr. Liebermann no ve caracteres morfológicos externos distintos de suficiente entidad como para diferenciar a *Dichroplus pratensis* Bruner con la nueva especie *Dichroplus silveiraguidoi*. Más adelante, sin embargo, presenta algunos caracteres diferenciales que parecería que no los considerara terminantes. Es aquí, donde la citología, con moderno concepto taxonómico, concluye que se trata de dos especies completamente distintas. Y es así pues que Liebermann, dice:

". . . tomamos en cuenta para su descripción una diferencia más fundamental que todas las mencionadas. Se trata de diferencias notables en el material cromosómico, en las que apoyamos nuestra determinación para considerarla como especie nueva". Las diferencias citológicas se dan a continuación:

Especie	Número diploide 2n(♂)	Número de metacéntricos	Cromosomas X	Número de brazos cromosómicos
D. pratensis Bruner	18	1	Libre	19
D. silveiraguidoi Lieb.	8	4	XY	12

Como puede observarse existen diferencias bien marcadas entre los cariotipos de las dos formas de *pratensis* y *silveiraguidoi* que hacen incompatible su cruza y mantienen por tanto su aislamiento.

El caso de *Dichroplus silveiraguidoi*, dice Saez (1956a, 1956b) es extraordinario al mostrar ocho elementos diploides, lo que significa que se han perdido once cromosomas del complejo original. En estos individuos el cromosoma sexual no se comporta como un elemento impar, dado que está asociado con un pequeño cromosoma con el que forma un bivalente acrocéntrico heterocigota, que se segrega en la primera división meiótica como un complejo X–Y determinante del sexo.

OBJETIVOS Y SUS FUNDAMENTOS

Dentro de la Biología, el significado de especie, la unidad base de la taxonomía, ha sido ampliamente discutido con el objeto de lograr una mayor exactidud.

Este trabajo está animado por el intento de pretensión de aportar un algo tendiente a esclarecer los límites de las especies de acridios del Uruguay, lo cual se incluye entre uno de sus objetivos.

Con sentido taxonómico en estrecha colaboración con el Prof. F. A. Saez, quien ha tenido la gentileza de estudiar las preparaciones microscópicas de gónodas masculinas preparadas en nuestra Cátedra de Entomología, se dá el resultado general de esta investigación dado a conocer en la Tabla I.

TABLA I.

Especies	Número diploide 2n(♂)	Número de metacéntricos	Cromosoma X.	Número de brazos cromosómicos
ACRIDINAE				
Dichroattetix bohlsi (Giglio-Tos) Lieb.	23	–	Libre	23
Hyalopterix rufipennis Charpentier	23	–	Libre	23
Staurorhectus longicornis Giglio-Tos.	23	–	Libre	23
Scyllinops bruneri (Rehn).	23	–	Libre	23
Scyllinops pallida (Bruner).	23	–	Libre	23
Rhammatocerus pictus (Bruner).	23	–	Libre	23
Amblytropidea australis Bruner.	23	–	Libre	23
Parorphula graminea Bruner.	23	–	Libre	23
Orphulella punctata (De Geer).	23	–	Libre	23
Dichromorpha australis Bruner.	23	–	Libre	23
Sinipta dalmani (Stal).	23	–	Libre	23
Laplatacris dispar Rehn.	23	–	Libre	23
Metaleptea brevicornis adspersa (Blanchard).	23	–	Libre	23
Allotruxalis strigata (Bruner).	23	–	Libre	23
CYRTACANTHACRIDINAE				
Neopedies brunneri (Giglio-Tos) Heb.	23	–	Libre	23
Scotussa lemniscata (Stal) Lieb.	23	–	Libre	23
Aleuas brachypterus Bruner.	19	4	Libre	23
Dichroplus punctulatus (Thunb.)	23	–	Libre	23
Dichroplus conspersus Bruner	23	–	Libre	23
Dichroplus elongatus Giglió-Tos	23	–	Libre	23
Dichroplus bergii Stal	22	1	Unido	23
Dichroplus pratensis Bruner	18	1	Libre	19
Dichroplus pratensis (?)	18	5	Unido	23
Dichroplus silveiraguidoi Lieb.	8	4	X–Y	12
ROMALEINAE				
Tropinotus fuscipennis Bruner	23	–	Libre	23
Elaeochlora viridicata (Serville) Stal	23	–	Libre	23
Chromacris speciosa (Thunberg)	23	–	Libre	23
Zoniopoda tarsata cruentata (Blanch) Rehn	23	–	Libre	23
Tropinotus laevipes Stal	22	1	Unido	23
Diponthus maculiferus (Walker) Stal	21	2	Libre	23
Atrachalacris unicolor Giglió-Tos	22	1	Unido	23
OMMEXECHINAE				
Ommexecha servillei Blanchard	21	2	Libre	23

De este cuadro surgió la afirmación de nuestra inquietud y la especie *Dichroplus silveiraguidoi* de Liebermann, creada cariológicamente por Saez. Es también de este mismo cuadro que se acentúan nuestras sospechas ya expuestas sobre distinción de la forma que llamamos *Dichroplus pratensis* (?) con respecto a *Dichroplus pratensis* Bruner, las cuales son consideradas por Saez, como cariotipicamente distintas. En este último caso sufrimos una indecisión para proceder a separar en especies (con criterio cariológico, tal vez se justificaría su separación) o bien dejarlas como están (la morfo-taxonomía así aconsejaría).

MATERIAL Y METODOS

El material insectos empleados para realizar este trabajo fué cazado con red común y luego matados en cámara letal a gas cianhídrico, excepto los individuos destinados a extraérseles las gónadas, los cuales fueron enjaulados vivos.

Una vez extraídas las gónadas de los individuos vivos, se fijaron en alcohol-acido acético (3:1), pasando luego de 6 horas a alcohol 70°. En el laboratorio se procedió a la hidrolización con ácido clorhídrico N/1, coloración con fuscina, etc. Se empleó la técnica de aplastamiento de Feulgen, y el montaje definitivo se hizo en aceite de cedro. Se hicieron 1.020 preparaciones microscópicas.

DISTRIBUCION GEOGRAFICA DE *D. SILVEIRAGUIDOI* Y *D. PRATENSIS*

Hasta ahora, con los datos que poseemos, la especie *Dichroplus silveiraguidoi* se distribuye dentro de un área muy restringida (v. Fig. 5), lo cual no acontece con la *D. pratensis* Bruner que está, practicamente, distribuída en todo el territorio de la República O. del Uruguay (v. Fig. 6).

Los puntos marcados en la Fig. 5 señalan las localidades: Cerro Batoví, zona Cerro Cuñapirú, Arroyo de la Invernada, punta Arroyo Laureles y Bajada de la Pena. Los tres últimos datos fueron proporcionados por el Ing. Agr. Carlos S. Carbonell, con fechas de caza de diciembre de 1953 y de 1954.

POBLACIONES DE *D. SILVEIRAGUIDOI*

Conviniendo que la nueva citología evolucionaria cree necesario establecer las dimensiones de las poblaciones de donde se extraen las muestras, queremos informar que las dimensiones de las poblaciones de *D. silveiraguidoi* las podemos considerar, con los datos que hasta ahora disponemos, bastantes reducidas, representando en la zona del Cerro Batoví (alrededor de un kilómetro cuadrado) una proporción aproximada de 1:5.000.000 con respecto al total de las otras especies de *Acridoidea*, en las que se incluyen las especies:—

ACRIDINAE: *Scyllinops bruneri* (Rehn), *Scyllinops pallida* (Bruner), *Parorphula graminea* Bruner, *Orphulella puntacta* (De Geer), *Rammathocerus pictus* (Bruner), *Staurorhectus longicornis* Giglio-Tos, *Allotruxalis strigata* (Bruner), *Dichroatettis bohlsi* (Giglio-Tos) Rehn, *Laplatacris dispar* Rehn, *Sinipta dalmani* (Stal), *Amblytropidia australis* Bruner, *Cocytotettix intermedia* (Bruner) Rehn.

CYRTANCANTHACRIDINAE: *Dichroplus pratensis* (Bruner), *Dichroplus consperuss* Bruner, *Dichroplus puntulatus* (Thunberg), *Dichroplus elongatus* Giglio-Tos, *Neopedies bruneri* (Giglio-Tos) Heb, *Scotussa lemniscata* (Stal) Liebermann, *Aleuas brachypterus* Bruner, *Aleuas lineatus* Stal, *Atrachelacris unicolor* Giglio-Tos.

ROMALEINAE: *Zoniopoda tarsata cruentata* (Blanchard) Rehn, *Eleaochlora viridicata* (Serville) Stal, *Diponthus maculiferus* (Walker) Stal.

OMMEXECHINAE: *Ommexecha servillei* Blanchard.

Por otra parte conviene decir que en el Cerro Batoví, una de las localizaciones citadas para la especie *D. silveiraguidoi*, la misma se hallaba relativamente aislada en el segundo escalón del cerro propiamente dicho, las paralelas confinan el lugar (v. Fig. 1). En tal pequeña área convive con el *cirtocanthacridino*, *Dichroplus pratensis* Bruner, según nuestros apuntes de febrero de 1955.

En la zona de la parte inferior de la horizontal más baja (v. Fig. 1) se encontraron las 25 especies que mencionan.

HABITAT, COSTUMBRES, CICLO BIOLOGICO DE *D. SILVEIRAGUIDOI*

La especie *D. silveiraguidoi* fué observada en ambientes denudados, pedregosos (graníticos o basálticos), altos, pocos protegidos de los vientos (ejemplo en cerro Batoví, Rivera). Las especies vegetales registradas en esta microzona fueron las siguientes:

Acanthospermum australe (L) O. Ktze., *Baccharis articulata* Pers., *Achyrocline saturejoides* (Lam), *Cynodon dactylon* (L) Pers., *Baccharis* sp.

Los individuos de *D. silveraguidoi* son muy movedizos, difíciles de cazar, sobre todo en las horas más cálidas. Sus saltos son de 5 a 7 metros.

Copula hasta muy entrada la tarde (II–1955, 7.30 p.m.).

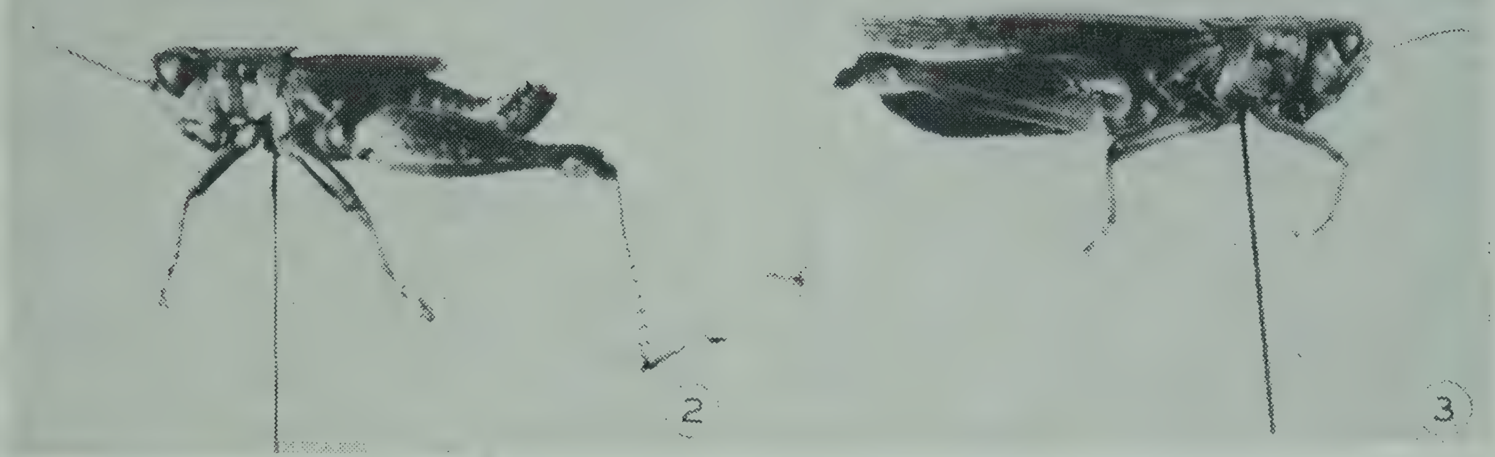

Fig. 1. Zona del Cerro Batoví (Rivera) sobre el que se localizó el *Dichroplus silveiraguidoi*.

Figs. 2–3. Vista lateral del macho de *Dichroplus* spp. 2, *silveiraguido*. 3, *pratensis*.

El material recogido por los autores, siempre en estado adulto, está en las fechas: 19–I–955, 4–III–955 y 24–III–956.–En las giras realizadas tanto en diciembre como a principios de abril no se hallaron individuos de la especie.

Aparentemente, pues, según nuestros datos la *D. silveiraguidoi* en estado adulto la tendríamos desde diciembre hasta mediados de marzo. Por otra parte tenemos a *D. pratensis* desde octubre hasta fines de abril, mes este último en el cual registramos parejas en cópula.

MORFOLOGIA COMPARADA

En la morfología comparada, entre las especies *Dichroplus pratensis* Bruner y la *D. silveiraguidoi* Lieb. las diferencias más notables las tenemos en el siguiente cuadro:—

	D. pratensis Br.	D. silveiraguidoi Lieb.
Largo total del cuerpo, promedio:	24.83 mm.	17.73 mm.
Largo total de la tegmina, promedio:	18.91 mm.	6.70 mm.
Cabeza	Diferencias no significativas	– – – – –
Antenas	25–segmentada	21–segmentada
Pronoto	Proporcionalmente la metazona es mayor para *pratensis* que para la cotejada.	– – – – –
Fúrcula tergal	Larga, fina, digitiforme.	Corta, ancha, subtriangular.
Cercis	Algo más robustos que en *silveiraguidoi*	Finos, delgados, más agudos que en *pratensis*.
Lóbulo esternal del IX	Ver fig. 10 B y 11 B	Ver figura 10 A y 11 A

Veáse Figs. 4, 5 y 7–11.

MORFOMETRIA COMPARADA

El estudio morfométrico entre las especies *D. pratensis* y *D. silveiraguidoi*, se expone en la Tabla II.

TABLA II.

PRONOTO			LARGO		CABEZA		LARGO DEL FEMUR			LARGO TOTAL	
Largo	Altura	Anch. Max.	Prozona	Metazona	Larg. Max.	Anch. Max.	Post.	Ant.	Medio	Cuerpo	Tegmina
					Dichroplus pratensis Bruner (hembras)						
5.99	4.42	3.42	3.00	3.00	6.42	4.71	15.56	3.85	4.85	26.84	20.56
5.99	4.28	3.07	3.00	3.00	6.57	4.71	15.13	3.42	4.71	24.56	20.27
5.00	3.85	3.00	2.57	2.42	6.14	4.42	13.13	3.00	3.71	24.42	16.13
5.85	4.42	3.00	2.85	3.00	6.71	4.71	13.99	3.07	4.42	23.56	18.70
5.71	4.42	3.35	2.92	2.78	5.92	4.71	15.13	3.71	4.28	25.70	20.13
					Dichroplus pratensis Bruner (machos)						
5.14	4.00	2.71	2.57	2.57	4.35	4.00	13.71	3.57	4.42	24.34	17.85
5.57	4.71	3.14	2.71	2.85	6.57	4.71	14.14	3.85	4.57	25.70	20.70
5.42	3.71	3.42	2.57	2.85	6.57	4.57	14.78	3.71	5.00	26.13	18.99
5.57	4.00	3.07	2.57	3.00	6.42	4.28	15.13	3.85	4.28	27.56	19.85
5.71	4.28	3.21	2.85	2.85	6.64	4.28	14.42	3.78	4.42	24.99	19.28
					Dichroplus silveiraguidoi Lieb. (machos)						
4.25	3.22	2.49	2.41	1.83	4.98	3.37	10.55	2.78	3.24	16.85	6.52
4.32	3.59	2.78	2.49	1.83	5.13	3.44	10.26	2.85	3.44	18.32	6.52
3.95	3.07	2.41	2.19	1.68	4.83	3.07	10.33	2.78	3.29	16.78	6.81
4.32	3.44	2.49	2.41	1.83	4.18	3.44	10.42	2.71	3.44	18.98	6.96
					Dichroplus silveiraguidoi Lieb. (hembras)						
4.83	3.95	2.85	2.56	2.05	5.64	3.95	13.12	3.07	3.59	21.11	7.33
5.49	4.54	3.44	2.85	2.56	5.71	4.17	12.53	2.85	3.59	22.13	7.98
5.71	4.61	3.81	3.07	2.63	6.30	4.54	13.41	3.07	3.88	21.62	8.57
5.71	4.54	3.51	3.07	2.56	6.45	4.17	13.14	3.07	3.81	20.08	

FINALIDAD DE ESTE TRABAJO

De resultancias de este trabajo se pretende deducir que sería conveniente, cuando de descripciones se trate, la colaboración estrecha entre el entomolögo y el citólogo, con discusiones fundamentales suficientes como para arribar a una conclusión, que en la peor circunstancia podría ser de índole convencional, con criterio tolerante por ambas partes.

REFERENCIAS

Hurst, C. C. 1933. The mechanism of creative evolution. Cambridge.

Saez, F. A. 1956a. Cytogenetics of South American Orthoptera. *Nature* 177.

Saez, F. A. 1956b. An extreme caryotype in an orthopteroid insect. Montevideo. (Inédito).

Silveira Guido, A., O. Nuñez, J. Carbonell, y E. Valdes, 1956. Estudio sobre veintiocho especies indígenas de *Acridoidea* de interés para el Uruguay. Montevideo. (En prensa).

Stebbins, G. L., Jr. 1950. Variation and evolution in plants. *Columbia University Press.* New York.

White, M. J. D. 1951. Citología animal y evolution. Buenos Aires.

DISCUSSION

F. G. Werner. I would like to call attention to the work of Dobzhansky *et al.* where chromosome polymorphism is possible in the same species. The methods used here are those of cytotaxonomy and I feel they may not indicate the whole situation. Cross-breeding experiments are certainly needed for a final decision.

Aquiles Silveira Guido. Estamos encarando el cross-breeding con *Dichroplus pratensis* Bruner, *D. pratensis* (?) y *D. silveiraguidoi* Lieb. por un lado y por otro *Scyllinops bruneri* Rehn y *S. pallida* (Bruner) Con el estudio citologico no tenemos duda de que *Dichroplus pratensis* Bruner (con 2 n (♂) / = 18) y *D. silveiraquidoi* (con 2 n (♂) / = 8). En esto hay seguridad. En otras especies se debe ir al numero de cromosomas, grado de concentracion de la cromatina, heteropicnosis, grado de epirilicacion. En individuos de distintos genes, estos pueden encontrarse ordenados de manera distinta debido a las alteraciones ocurridas en los segmentos cromosomicos, verdaderas mutaciones que desempeñan un papel preponderante en el mecanismo de la formacion de la especie.

Los trabajos citologicos de Dobzhansky son muy importante.

Pensamos que mas adelante la especie sera definida por sus caracteres cariologicos.

Cl. Dupuis. L'étude de la durée relative des stades larvaires pourrait constituter un intéressant caractère additionnel pour la différenciation des espèces sur d'autres bases que morphologiques et cytologiques (cf. travaux de R. Sellier sur *Gryllus*).

Aquiles Silveira Guido. Muy probablemente si, aun no hemos trabajado en este terreno.

Section

on

MORPHOLOGY AND ANATOMY

◆

Section Editor

J. R. Vockeroth

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The Nervous System of Insects

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Before entering upon any discussion of the nervous system of the insects it is desirable, or even necessary, first to discuss the general principles which, it seems to me, should guide us in its investigation. Unfortunately, it seems from a review of the work that has been done, that much of this work has been developed without the benefit of any clear and definite principles. Much of its has been merely the recital of what is to be seen in a single insect species considered entirely as an isolated object and without any reflection upon the question of its relation to other insects or to what it may have been derived from. Very little of this work has considered, in some intelligible manner, any insect as a member of an evolutionary series from which it has arisen. The literature on the nervous system of insects is extensive and it may very well be that in reviewing it I have overlooked studies of the desirable kind. If so, I can do no more than apologize to whomever I have done an injustice and maintain that such injustice has been wholly unintentional and without malice aforethought. However, a consideration of the one general work, Hanstroms' book on the nervous system of the invertebrates, of as late as 1928, in which previous literature is treated very thoroughly, does not indicate that any serious injustice has been done.

As a result of this piecemeal and uncoordinated work, there has appeared a body of published fact or supposed fact concerning the nervous system of insects that leaves a considerable number of matters, some of them vital for a clear understanding, but little considered of even not considered at all.

I have consequently been faced with the necessity of formulating a set of principles which should guide our work in comparative morphology. I must at once frankly admit that I have, myself, at times paid insufficient attention to my own principles, but that does not change the principles or diminish their applicability. A brief review of these principles may be presented as a background for what I have to say concerning the nervous system of insects.

There is first of all one general principle which applies to all scientific work, of whatever kind it may be, whether astronomical, physical, chemical or biological. That is the principle that there is, fundamentally, order in all things, living and non-living [barring only a disorder in the atomic realm but which, even here, results in statistical order]. In other words, all observable processes can be reduced to consistent systems. There are no miracles.

This principle has, in effect, been tacitly denied at times and by many people in the field of biology. There has long persisted among biologists, or those merely on the fringe of biology, the feeling that living things do not conform to this principle, that living things are erratic, doing now this and now directly the contrary, with no hope of reducing their behavior to any common basis. This belief arises from that dualism of life and matter which has been commonly held. The steady advance of biochemistry and biophysics into hitherto unexplorable, or at least unexplored, fields of biology is adequate assurance that this is not true. The function of scientific work is to reduce all things to order and that function is slowly but surely being attained in the realm of living things.

There is the principle that a mass of disconnected facts cannot be reduced to order by the simple contemplation of facts alone. Let us keep in mind the observation credited to J. H. Huxley to the effect that he who claims never to deal with anything but facts rarely gets as far as the facts. There must be the vision of and the establishment of hypotheses by which the observation and interpretation of facts can be guided. Any hypothesis may eventually prove to be ill-founded—as has very frequently been true—but there must be some hypothesis with which to begin our work.

We accept the hypothesis of organic evolution as the most reasonable one upon which to base our work in reducing the vast body of facts concerning living things to some order and system. We must, in comparative morphology, assume that evolution has had a certain order, each step conditioned by and arising from what has preceded that step. It may finally prove that this assumption is wrong, but we must employ it, at least initially and until it is demonstrated to require modification. To assume otherwise, that it has been disorderly and disconnected in its various stages, is to cut ourselves off from ever attaining anything more than that with which we began—a set merely of disconnected facts.

When we attempt to apply these principles to the limited field of comparative morphology there are certain more limited principles or axioms or assumptions—call them what you will—that must be taken into consideration.

First, we must be able to rely upon our facts. Every structure that can be seen with the aid of the best equipment and the best techniques available must be seen and seen correctly.

Then every structure that can possibly be concerned with the question at hand must be taken fully into consideration. Nothing may be casually dismissed as "merely there."

It must be recognized that comparative morphology cannot be merely the factual comparison of the end products of evolution, one directly with another. Little or nothing is to be gained by the direct comparison of highly specialized forms. The comparison should be with less specialized forms.

Apparent discrepancies must be most respectfully approached and must eventually be explained. There is nothing so good as a glaring discrepancy to stimulate further work. In the words of Sir Patrick Manson, "It is the discrepancy that teaches, if you would learn." In attempting to account for an apparent discrepancy it is a justifiable procedure to first assume somewhere an error of observation. If this possibility has been eliminated the existence then of an error of interpretation is next to be considered. If this is eliminated it would seem that we do not yet have all the pertinent evidence. And if the discrepancy still persists—well, it is the fate of unsolved problems some time to be solved.

In accord with these principles we may formulate certain postulates.

We postulate that evolution has in general proceeded by relatively small steps. The complete acceptance of Goldschmidt's idea of macroevolution would seem to make the achievement of a comparative morphology impossible. "There was a dinosaur, there was a dinosaur's egg, there was a bird." We cannot base comparative work on such an idea.

We postulate that all changes have taken place in accord with the Mendelian laws of genetics, as they are known or as they may come to be known. There should be no place in our work for the slightest vestige of Lamarckism. Function merely makes use of what is provided for it.

We postulate that evolutionary changes are first to be accounted for by changes in the proportions or development of preexisting parts, by the fusion of preexisting parts, or by the loss of preexisting parts. Rarely and only as a last resort will we be forced to conclude that something quite new and entirely unrelated to any preexisting structure has developed.

And last of all, we postulate the justification for a faith that somewhere in the great mass of material presented to us by the annulates there will lie hidden a reasonable answer to any question that may arise.

Thus armed with a set of principles and postulates and the corollaries that may be derived from them, we may at last proceed to approach the problems of the comparative anatomy of the nervous system of insects.

The basic pattern of this nervous system is well enough known. It is in regard to the elements of this pattern that there is still difference of opinion.

What, for example, is the relation of the nervous system to segmentation and what light does the nervous system throw upon the segmentation of the various body regions?

Evidently this cannot be determined directly from existing insects, to which many things have happened in the course of their evolution of hundreds of millions of years. In the higher insects especially there has been a fusion of parts and an elaboration of certain parts to such a degree that no conclusions can be drawn directly from, for example, a honey bee. The direct comparison of a honey bee and a fly can give us nothing more than the most general resemblances. We must go back and search for the general system that underlies such forms; if possible, we must go back to the basic system of all arthropods.

In such a matter as this the earlier studies of the nervous system are to a very large degree inadequate. They have failed to take into consideration that basic system from which the nervous system of our present day insects must have been derived.

For example, how many segments are there in the insect head and what is the relation of the nervous system to these segments? It seems to me that the nervous system represents the last available system of the body that can throw any light upon this question. And it seems to me that few, if any, existing studies that have considered this question have done so in the light of principles which embody the thoughts that I have presented.

It may be said immediately that, studied as they usually have been, that is, as detached and isolated objects, the nervous system and its parts offer nothing that can be relied upon to give an answer to the question of the segmentation of the head. The idea seems to have prevailed that the nervous system, is at least in its details, subject to vagaries that entirely destroy any value that it might have for comparative morphological work on such a subject as the segmentation of the head. Thus, our most distinguished American student of comparative morphology has paid much attention to the muscles, but very little attention to the nerves that innervate those muscles. It seems to have been concluded that the nervous system and the muscles have little in common except that "a muscle has to be innervated from somewhere."

I submit that such a conclusion is not justified by the work that has been done thus far and that it will remain unjustified until the nervous system has been studied in the light of the principles that I have enunciated. I submit that when the nervous system has been adequately investigated in that light most of the difficulties which will be found will fade away and it will become as intelligible and as orderly as any other system of the insect body.

But with what should we begin this work?

In the present state of our knowledge we must begin somewhere in the annelids, the segmented worms, which offer us the only apparent source for the arthropods, specifically the polychaetes, for these are the only source that has been suggested.

However, I have been led to believe that the oligochaete worms are simpler than are the polychaetes and throw a very considerable light on the latter, for some oligochaetes present what is practically a duplicate of what has long been considered to be the basic plan for all of the annulates. They differ from the polychaetes, however, in not possessing the structure called the prostomium. Reasoning from the oligochaetes to the polychaetes I have been led to the belief that the prostomium of the polychaetes is not the same structure as that commonly called the prostomium in the oligochaetes. Work by one of my students, at present unpublished but to be published soon, indicates that here I violated some of my own principles and went seriously into error. In short, this matter is one that will demand much more study and reflection. We may leave it for the future.

The insect head, beginning with the antennae and extending to and including the labrum is currently accepted as being homologous to the prostomium of the polychaetes and to represent a single segment, if the term segment may be applied here. But here we encounter a very grave discrepancy which must be resolved if we are to gain an understanding of the insect head.

The discrepancy is this.

The prostomium of polychaetes, is supposed to be the anteriormost part of the body; there are no segments anterior to it.

But evidence from the work of more than one trustworthy student of insect embryology has shown that there are two coelomic sacs anterior to the antennae in the embryos of insects and the work of one of my own students has shown that there is certainly at least one sac in this position in the Anoplura. If this be true, then certainly this area in the insects can not be homologous with the prostomium of the polychaetes. I may add that from my own point of view the evidence from external morphology supports the belief that there are such segments in the insects and everything that I have seen in the distribution of the nerves in the insects conforms very easily to and supports this. The distribution of the nerves indicates clearly that the insect head is composed of six segments, the labrum, the clypeus, the ocular-antennal segment, the mandibular segment, the maxillary segment and the labial segment.

I still think that this discrepancy can be resolved by work on the polychaetes which will demonstrate that their prostomium is not the anteriormost point of the body and that there are two segments anterior to it. Should this finally prove to be the case the nervous system of all the annulates will fall into one unified and consistent system.

There are still some things that have not been fully accounted for in the nervous system of the insects, that I know, but time does not permit the discussion of these matters. Perhaps some of the small discrepancies will eventually be resolved by further study. Perhaps some of them result from causes which are at present still beyond our ken, but I remain most sincerely convinced that, in conformity with other sciences, we must attempt to reduce the phenomena with which we deal to an internally consistent system and that we shall never arrive at a correct understanding of insect morphology in all its parts until we have done so.

Another Approach to Head Segmentation in Insects and other Arthropods[1]

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In choosing the title for this paper I did not have in mind another approach to head segmentation in the sense that this study is a new concept. Instead I wish to present another view of one of the toughest problems confronting the morphologist today—what constitutes the region of the mouth?

Before discussing the segmentation of the arthropod head one should consider the term "segment" in relation to the whole development of the arthropod from the early embryonic germ band to the full grown adult. We are interested in the primary body segment or "somite" known in the embryo as the "metamere." At some time during the development of the animal a segment bears a pair of appendages consisting, at the minimum, of transitory lobes; it contains early in development a pair of coelomic sacs; and it normally includes a ganglion forming a part of the central nervous system.

The early germ band consists of a heart shaped thickening (Fig. 1) very similar to the diagram of Krause (1938). This is the usual form of the germ band though in some insects the shape varies to a considerable degree. In *Oncopeltus* (Butt 1949) the germ band invaginates into the yolk except for the expanded head lobes which remain on the surface at the posterior pole (Fig. 2). When the embryo reaches its greatest length, segmentation begins as transverse grooves in the ectoderm first in the thoracic region (Fig. 3). It spreads from this point forwards and later backwards. The labral lobes appear widely separated before the stomodaeum forms (Figs. 3, 4). As the stomodaeum develops these lobes move around it and fuse to form the upper lip (Fig. 5). The bilobed nature of the labrum continues to be evident for a considerable length of time before it starts to form the elongate shape it finally assumes (Fig. 6). The labral lobes have well defined coelomic sacs, and have nerve connections with the tritocerebral lobes of the brain.

This development has been illustrated in the works of many authors over the past 75 years. It has been demonstrated in *Pyrilla* of the Homoptera by Sander (1956). In the Coleoptera it has been figured for *Dytiscus* by Blunck (1914) and Korschelt (1912), in the Lampyridae by Williams (1916), in *Silpha* by Smreczynski (1932), in *Brachyrhinus* by Butt (1936), and in *Calandra* by Tiegs and Murry (1938). In the Lepidoptera it has been shown very clearly by Johannsen (1929), by Rempel (1951), and by Rutschky and Presser (1957).

In the spiders it has been very clearly demonstrated in *Lactrodectus mactans* by Rempel (1957), in *Thellyphonus caudatus* by Kastner (1949), and in *Epiera cinera* by Lambert (1909). The labrum of spiders and mites is known as the rostrum; the chelicerae, though often taken for the equivalent of the antennae in insects, actually represent the mandibles, and the pedipalpi correspond to the maxillae.

In the Crustacea the second antennal appendages develop from the tritocerebral segment, only the triangular base of each appendage fusing to form the labrum as illustrated by Sollaud (1923).

In *Pauropus* of the Myriopoda these lobes never develop, but ventral organs, which migrate around the stomodaeum onto the under side of the upper lip, may be made out according to Tiegs (1947).

Cephalic migration of the ganglia of the labral or tritocerebral segment in the Hymenoptera is illustrated by Nelson (1915) who says that the appendages of this segment are in fact nothing more nor less than the second antennae of Butschli or the transitory anterior appendage of Grassi. Others who have illustrated the development of the labrum in the Hymenoptera are Schnetter (1934) and Bronskill (1957).

The movement of the tritocerebral lobes in a forward direction and the migration of the labral appendages around the mouth simply represent the instigation of cephalization. In some beetles this process continues until all the ganglia are located in the thorax in one large mass.

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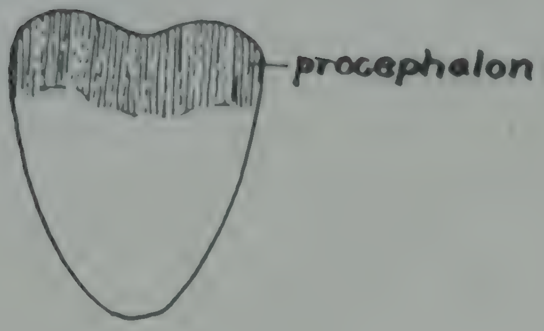
[1] Published under a similar title in *Trans. Amer. Ent. Soc.* 83: 1–30. 1957.



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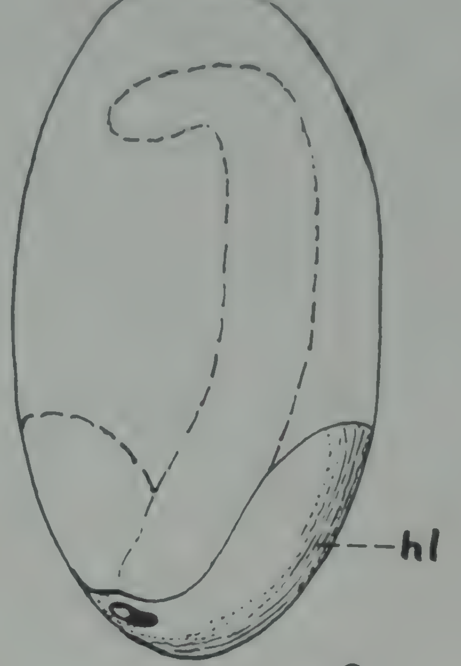

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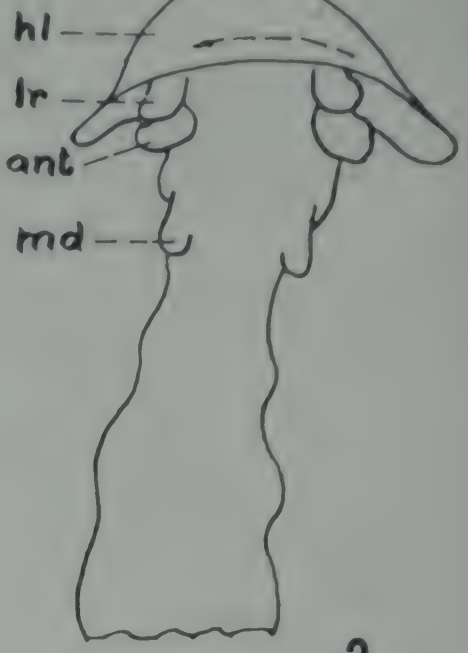

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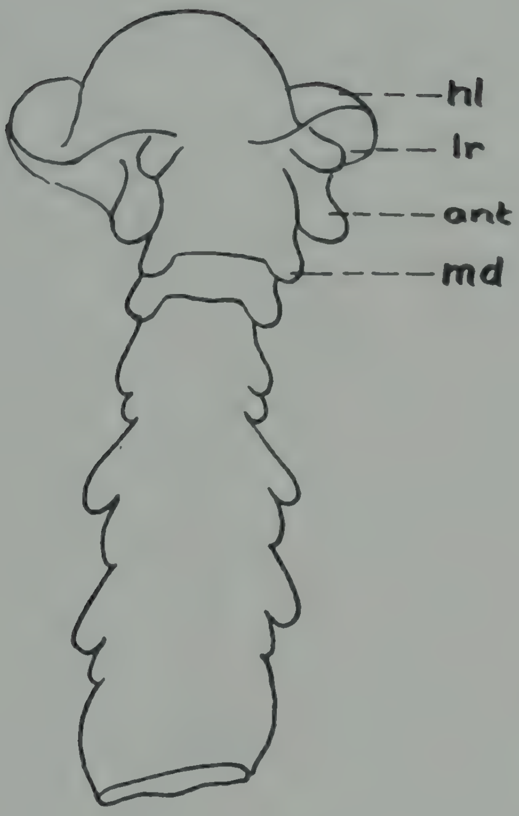

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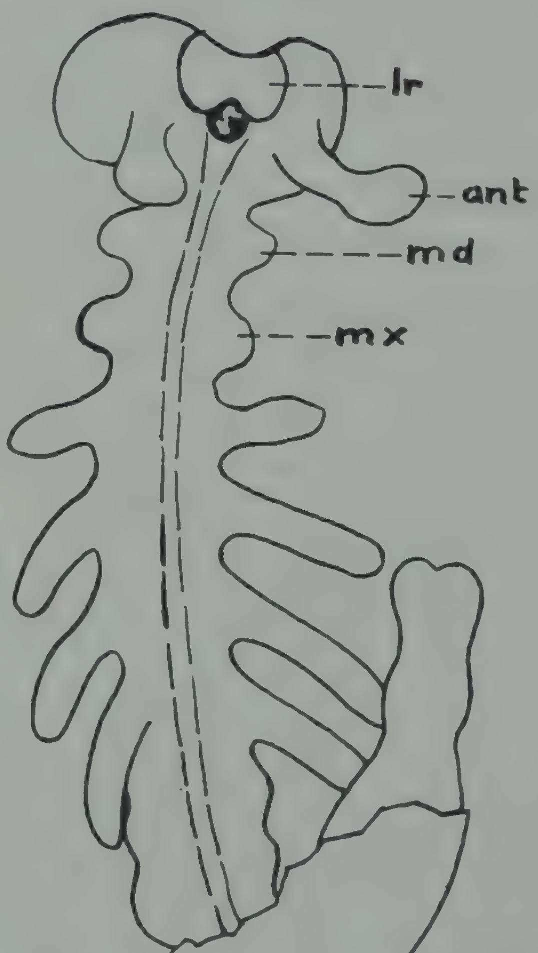

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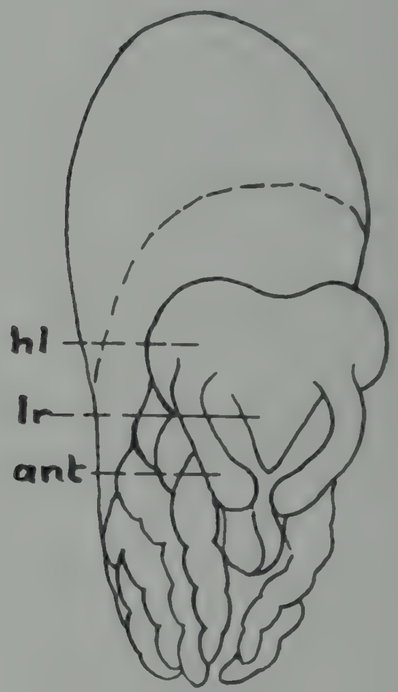

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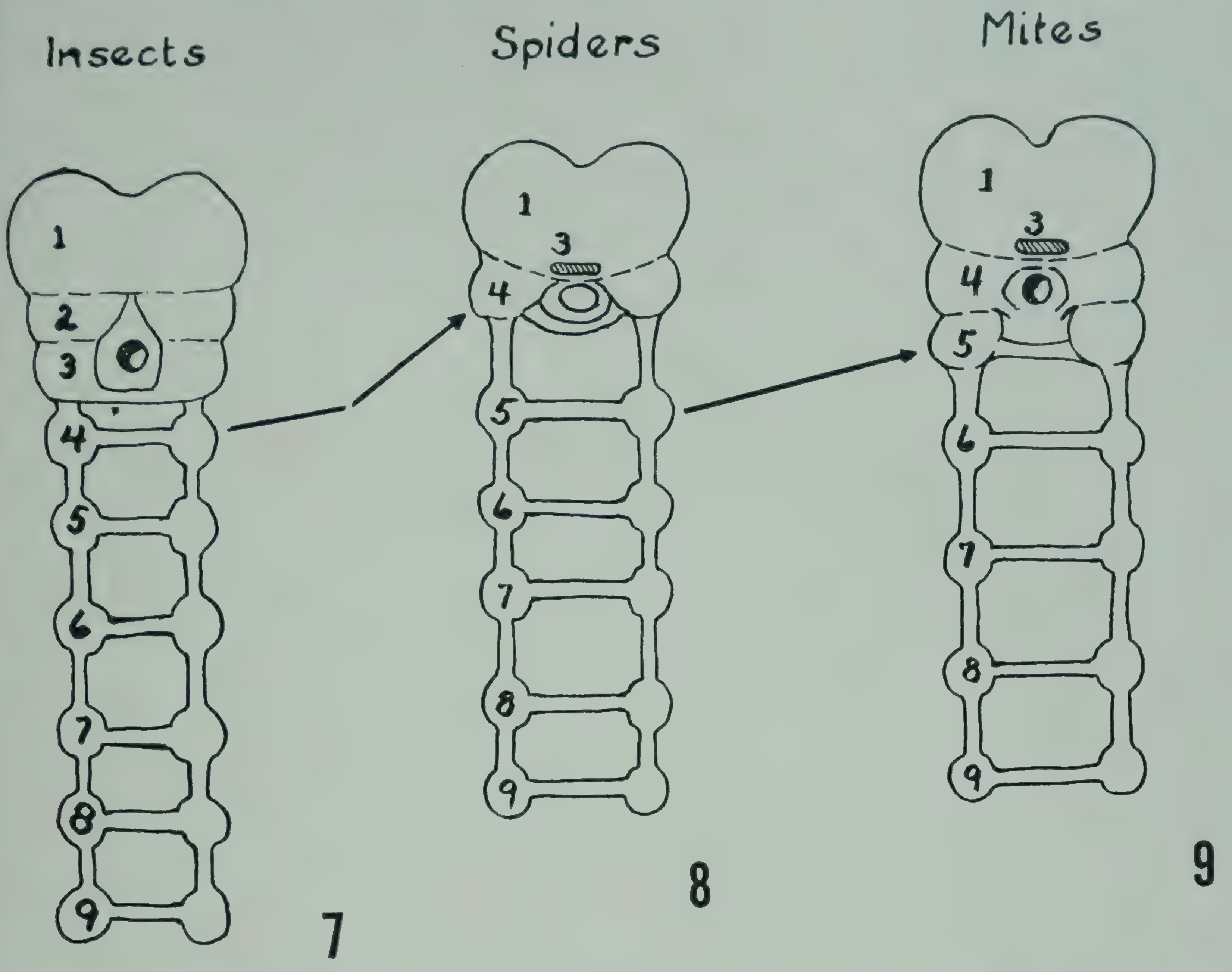
Fig. 1. Early embryo of *Tachycines*, from Krause (1938).

Fig. 2. Invaginated embryo of *Oncopeltus* with head lobes on the surface at posterior pole of egg, from Butt (1949).

Figs. 3, 4, 5, 6. Later embryos of *Oncopeltus* showing development of segmentation and appendages, from Butt (1949).

Abbreviations: abd, abdomen; ant, antenna; hl, head lobe; L, labrum (of Seidel); lr, labrum (rostrum); md, mandible; mx, maxilla; o schl, Oberschlundganglien (of Seidel); stom, stomodaeum; th, thoracic segment.

In spiders, according to Hanstrom (1928), the deutocerebrum and the antennae are missing, the brain consists of the protocerebrum, and the tritocerebrum which is much reduced consists of the protocerebral bridge only, with the cheliceral ganglion representing the fourth lobe. The chelicerae migrate around the stomodaeum and in front of the rostrum. In mites cephalization has progressed farther. The lobes of the fourth segment move still farther forward and their post oral connective becomes indistinct; the lobes of the fifth segment move up to take their place laterad of the mouth opening. The central nervous system of insects, spiders and mites are illustrated in Figs. 7, 8, 9 indicating the extent of cephalization in these forms. In *Limulus*, as in the spiders, the stomodaeal bridge, repre-


Insects
Spiders
Mites
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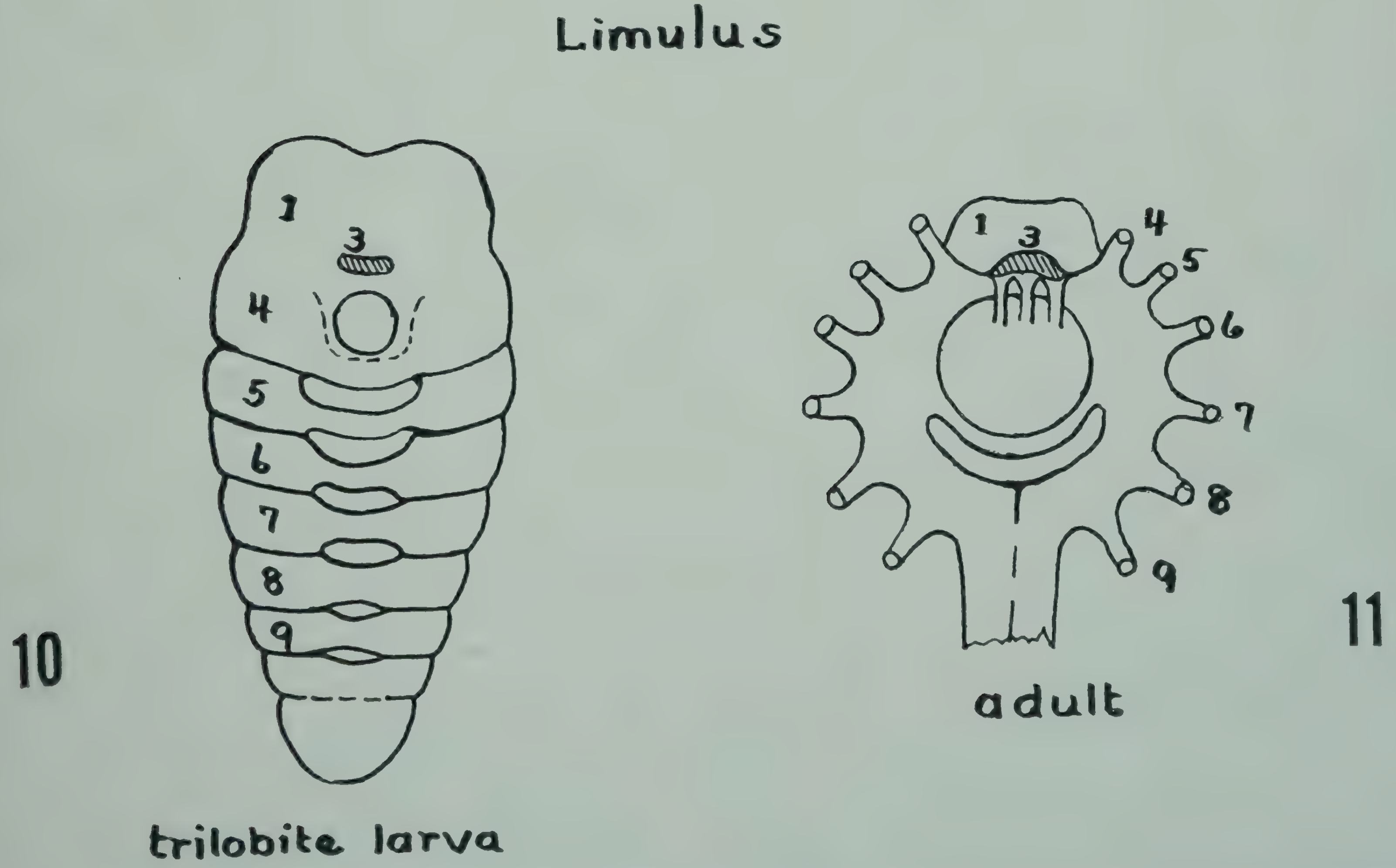
Limulus
1
3
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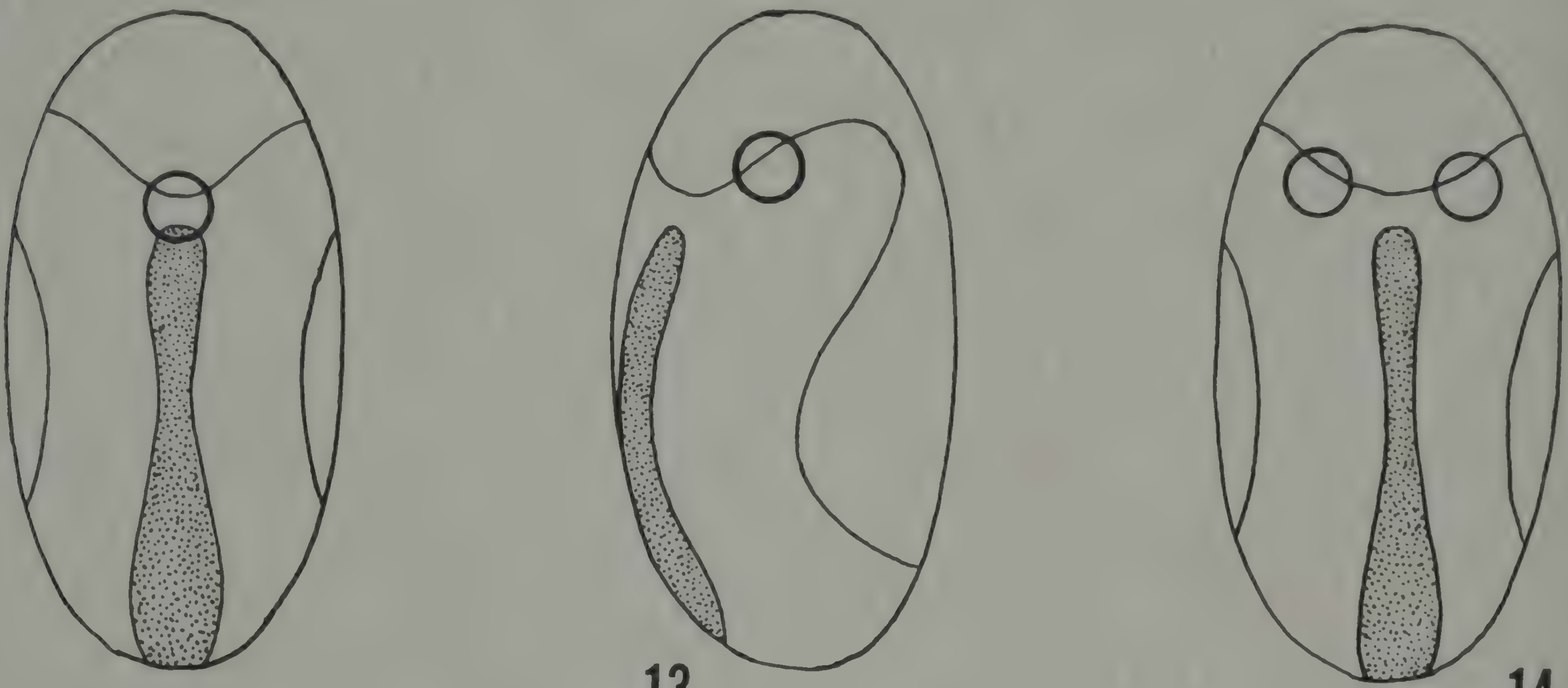
10
11
trilobite larva
adult

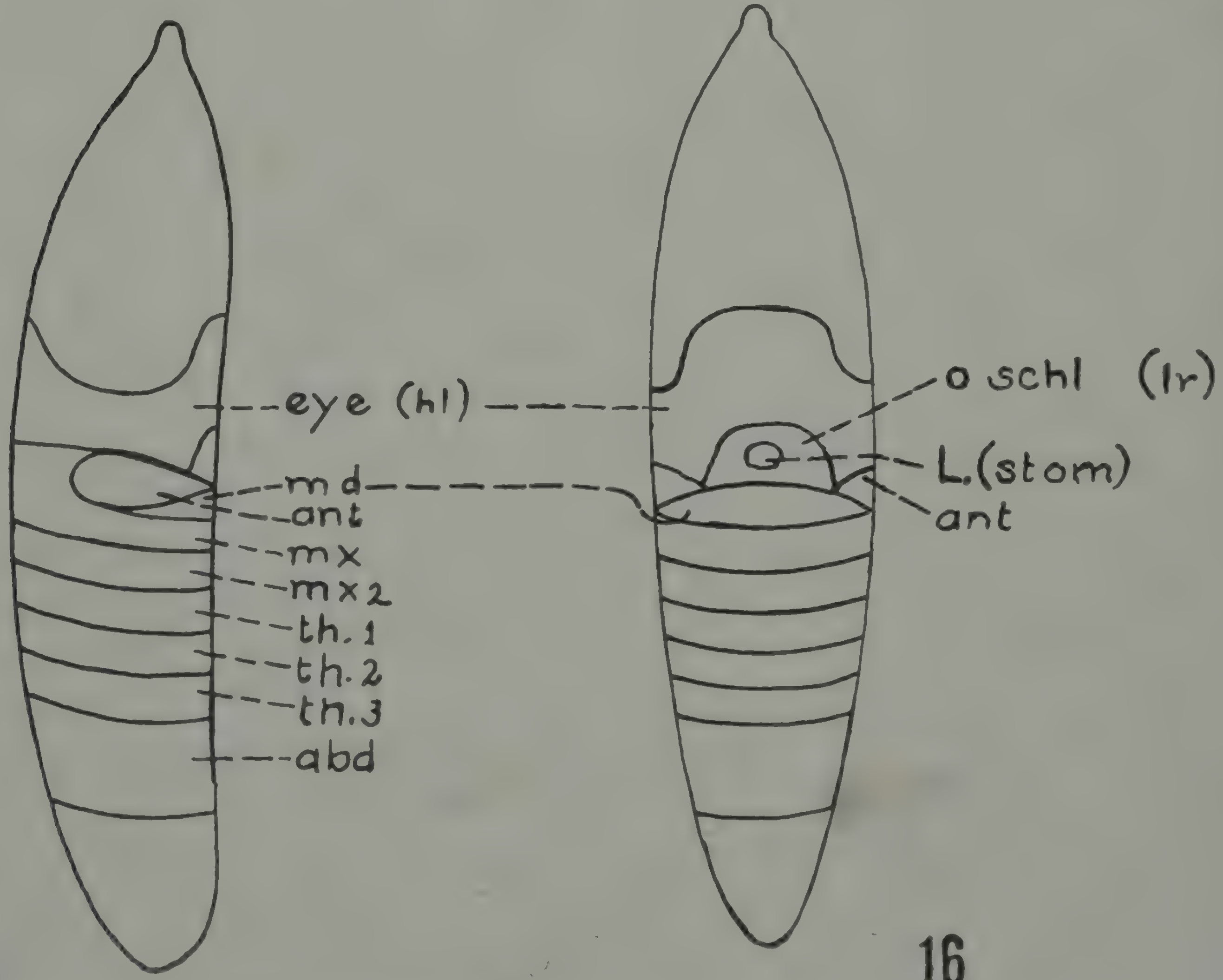
Figs. 7, 8, 9. Diagrams of central nervous system of insects, spiders and mites, indicating extent of cephalization in these forms.

Figs. 10, 11. Diagrams of central nervous system of *Limulus* larva and adult, indicating extent of cephalization in this form. Adapted from Hanström (1928).

senting all that is left of the tritocerebral lobe, is present and segment four and five have moved forward around the mouth, and six is on its way (Figs. 10, 11). Thus the process of cephalization reaches its highest degree of specialization in *Limulus*, the horse shoe crab.

It seems very improbable that entomologists will ever agree on the evidence for head segmentation from descriptive embryological studies such as I have presented here, and the only hope for new evidence lies in the work of the experimental embryologists. By destroying the ectoderm in front of the stomodaeum at an early stage in *Leptinotarsa* (Fig. 12), then to one side (Fig. 13) and finally on both sides (Fig. 14), Haet (1955) was able to trace the movement of the labral lobes and to determine that they have a paired origin. In these embryos the labrum was only half formed on that side which had not been cauterized, and in the last experiment where both sides were destroyed no labrum was formed at all.





Figs. 12, 13, 14. Diagrams to indicate experiments of Haget on labrum of *Leptinotarsa*. Areas cauterized, encircled stippled areas, mesendoderm.

Figs. 15, 16. Lateral and ventral views of *Platycnemis* egg, showing presumptive organ anlagen for the blastoderm stage, from Seidel (1935).

See explanations of Figs. 1–6 for abbreviations.

Seidel (1935) has presented an anlagen plan for the indeterminate or incompletely determinate type of insect egg using *Platycnemis*, one of the Odonata. In diagramming the presumptive organ areas in the blastoderm (Figs. 15, 16) these areas, in arrangement, bear a remarkable resemblance to the later arrangement of the embryo after the organs have begun to form. In the blastoderm the antennae are evident at the posterior edge of the area that will form the head lobes, and the area of the intercalary or labral segment or, as he calls it, "the supra oesophageal ganglion", surrounds the mouth opening. Unfortunately the island of material which he labels the labrum (Figs. 16, 1) appears incorrectly interpreted if we are to accept Haget's evidence and I think it should be considered the anlagen of the stomodaeum.

Ake Holm (1952) has used a method of marking areas of the embryo with stains instead of producing irradiation injuries as did Seidel. His method employed on spider embryos had no bearing on the problem with which we are concerned but it seems to be a method that has promise and could be applied in similar studies on the problem of cephalic migration in the insect egg.

REFERENCES

Blunck, Hans. 1914. Die Entwicklung des *Dytiscus marginalis* vom Ei bis zur Imago. I Teil. Das Embryonalleben. *Zeitsch. f. Wiss. Zool.* 111: 76–151.

Bronskill, Joan. 1957. The embryology of the pupal parasite *Pimpla turionellae* (L) with special reference to the migration of the germ cells (Hymenoptera: Ichneumonidae). (Unpublished ms.).

Butt, F. H. 1936. The early embryological development of the parthenogenetic alfalfa snout beetle, *Brachyrhinus ligustici* (L). *Ann. Ent. Soc. Amer.* 29: 1–13.

Butt, F. H. 1949. Embryology of the milkweed bug, *Oncopeltus fasciatus* (Hemiptera). *Cornell Univ. Agr. Exp. Sta. Memoir* 283: 43 pp.

Haget, A. 1955. Expériences mettant en évidence l'origine paire du labre chez l'embryon du Coléoptère *Leptinotarsa. Société de biologie de Bordeaux* 149: 690–692.

Hanstrom, B. 1928. Vergleichende Anatomie des Nervensystems der wirbellosen Tiere. Berlin.

Holm, Ake. 1952. Experimentelle Untersuchungen über die Entwicklung und Entwicklungsphysiologie des Spinnenembryos. *Zoologiska Bidrag fran Uppsala* 29: 293–424.

Johannsen, O. A. 1929. Some phases in the embryonic development of *Diacrisia virginica. Jour. Morph.* 48: 493-541.

Kastner, A. 1949. Zur Entwicklungsgeschichte von *Thellyphonus caudatus* L. (Pedipalpi). 2. Teil. Die Entwicklung der Mundwerkzeuge, Beinhuften und Sterna. *Zool. Jahrb. Jena* (*Anat.*) 70: 169–197.

Korschelt, E. 1912. Zur Embryonalentwicklung des *Dytiscus marginalis. Zool. Jahrb. Supplement* 15: 499–532.

Krause, G. 1938. Die Ausbildung der Korpergrundgestalt im Ei der Gewachschauschrecke *Tachycines asynamorus. Zeitschr. Morph. Oekol. Tiere* 34: 499–564.

Lambert, A. E. 1909. Procephalic lobes of *Epiera cinera. Jour. Morph.* 20: 413–460.

Nelson, J. A. 1915. The embryology of the honeybee. *Princeton Univ. Press.*

Rempel, J. G. 1951. A study of the embryology of *Mamestra configurata* (Walker) (Lepidoptera, Phalaenidae). *Canad. Ent.* 83: 1–19.

Rempel, J. G. 1957. The embryology of the black widow spider, *Latrodectus mactans* (Fabr.). *Canad. J. Zool.* 35: 35–74.

Rutschky, C. W., and Bruce Presser. 1957. The embryonic development of the corn earworm. *Ann. Ent. Soc. Amer.* 50: 133–164.

Sander, Klaus. 1956. The early embryology of *Pyrilla perpusilla* Walker (Homoptera) including some observations on the later development. *Aligarh Muslim University Publication* (*Zool. series*) 4: 1–61.

Schnetter, Martin. 1934. Morphologische umtersuchungen über das Differenzierungzentrum in der Embryonalentwicklung der Honigbiene. *Zeitschr. Morph. Oekol. Tiere* 29: 114–195.

Schnetter, Martin. 1934. Physiologische Untersuchungen über das Differenzierungzentrum in der Embryonalentwicklung der Honigbiene. *Arch. Ent.–Mech. Entwicklungsmediam* 131(3): 285–322.

Seidel, F. 1935. Der Anlagenplan in Libellenei, zugleich eine Untersuchung über die allgemeinen Bedingungen für defekte Entwicklung und Regulation bei dotterreichen Eierei. *Arch. Ent.–Mech. Entwicklungsmediam* 132: 671–751.

Smreczynski, S. 1932. Embryologische Untersuchungen über die Zusammensetzung des Kopfes von *Silpha obscura* L. *Zool. Jahrb.* (*Anat.*) 55: 233–314.

Smreczynski, S. 1932 (1931). Embryologische Untersuchungen über die Entwicklung des Kopfes von *Silpha obscura. Bull. Intern. Acad. Sci. Cracovie* 2: 649–651.

Sollaud, Edmund. 1923. Recherches sur l'Embryogénie des Crustacés Décapodes de la sous-famille des "Palaemoninae". *Bull. Biol. France et Belgique, Suppl.* 5: 1–234.

Tiegs, O. W. 1947. The development and affinities of the Pauropoda, based on a study of *Pauropus silvaticus. Quart. Jour. Micr. Sci.* 88: 165–336.

Tiegs, O. W., and F. V. Murry. 1938. The embryonic development of *Calandra oryzae. Quart. Jour. Micr. Sci.* 80: 159–284.

Williams, F. X. 1916. Photogenic organs and embryology of lampyrids. *Jour. Morph.* 28: 145–207.

Are There Preoral Structures in Insects[1]

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ABSTRACT

A brief summary of some theories of head structure precedes a critical discussion of Ferris and Henry's theory of the metameric organization of the polychaete proboscis, its supposed contribution to the head of arthropods and the apical position of the mouth in annelids and arthropods.

It is contended that phylogenetic and embryological evidence show that the primitive position of the mouth in bilaterally symmetrical animals is ventral and is posterior to the principal nerve centre, that nowhere in the literature of the Polychaeta is there any evidence of invaginated anterior segments such as claimed by Ferris and Henry, that there is direct evidence of the preoral position of the prostomium in annelids, and that Henry's evidence for the metameric constitution of the proboscis is inconclusive.

This evidence is based on the distribution to the proboscis of nerves branching from the circumoesophageal nerve cord, but this cord is formed by fusion of two components, the circumoesophageal connective and the stomodaeal commissure. Henry has not proven that the nerves in question arise from the connective, in which case they may be segmental nerves, and not from the commissure, in which case they are certainly stomodaeal nerves.

The weight of evidence therefore supports the generally accepted interpretation (1) that the proboscis is stomodaeal in origin, (2) that the prostomium is preoral in position, and (3) that the contributions of the prostomium to the insect head are also preoral in position.

INTRODUCTION

Theories of the origin of arthropods trace the origin of the phylum back to an annelidan or protoannelidan stock, and agree that the head in insects and other arthropods is the result of cephalization and concrescence of some of the anterior segments of their annelidan ancestors. We do not certainly know that the common ancestors of annelids and arthropods had a prostomium like that of present-day annelids, but the structure of primitive bilaterally symmetrical animals and the structure of the head in arthropods suggest strongly the presence in the ancestry of the latter of an apical region comparable to the prostomium.

Authors in general interpret the prostomium as a nonmetameric preoral region, but Ferris and his associates claim that in the Polychaeta the prostomium is a dorsal lobe of the third metamere and that the true mouth is the apical orifice of the extended proboscis, therefore there are no preoral structures in these annelids or in their derivatives the Arthropoda. This paper is concerned with an analysis of the evidence for their theory.

THEORIES OF THE POSITION OF THE MOUTH

Most writers believe that the mouth in arthropods lies in the first true metamere, the peristomium of the annelids, or between it and the prostomium; therefore any head structures derived from the prostomium are preoral. There is some difference of opinion as to the extent to which the prostomium contributes to the structure of the head. If, as some believe, prostomial elements are absent from the head, the mouth by implication is secondarily apical.

Lankester (1881) believed that the mouth in Crustacea has migrated backwards to the third segment and, as a result, the first and second antennal segments, primitively postoral, assume a preoral position. He believed that the "ophthalmic segment" is derived from the prostomium and is therefore morphologically preoral. This theory has been widely adopted by entomologists who have claimed that the "antennal segment" is derived from a postoral metamere of the annelids and that its definitive preoral position is secondary. Hanström (1928), however, concluded from his comparative study of the nervous system that the deutocerebrum is not a segmental ganglion but corresponds to nerve centres associated with sense organs in the prostomium of the Polychaeta. The antennae, therefore, are derived from prostomial organs and there is no antennal metamere. This suggests that

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[1] Contribution from the Faculty of Agriculture, McGill University, Macdonald College, Que., Canada.

the oculo-antennal region and possibly the clypeus are preoral. The homology of the labrum is somewhat doubtful. It is usually regarded as an apical lobe of the prostomium, but if the mouth has not shifted its position it should open in the first metamere and there is a possibility that the labrum belongs to this oral segment.

Snodgrass (1938) has accepted and amplified Hanström's theory but many embryologists do not accept it. It is important to remember, however, that Ferris and Henry accept the theory of the prostomial origin of the oculo-antennal region of the arthropod head though they reject the view that the prostomium is preoral.

Ferris (1942), from a comparative study of the insect head, came to the conclusion that the labrum is the apical segment of the head, that the mouth opens in this segment and, consequently, there are no preoral structures. This conclusion seemed to be confirmed by evidence obtained in his laboratory by Henry (1947, 1948) as the result of a careful and detailed study of the nervous system of the anterior region of the Annulata. From these studies Ferris and Henry reached the radical conclusion that the proboscis in the Polychaeta is not an eversible region of the stomodaeum, but consists of three invaginable body segments, and that the apical orifice of the extended proboscis is the true mouth. The prostomium, they claim, is not preoral, but is a dorsal lobe of the third segment of the proboscis. These authors believe that arthropods are descended from polychaete annelids and claim, from their comparative study of the nervous system, to have succeeded in identifying the three segments of the polychaete proboscis in the head structure of insects and other arthropods. They claim further that the mouth in arthropods is apical because it opens in the "labral segment" which they identify as the first segment of the polychaete proboscis.

Henry's comparative studies of the nervous system in the annulates is a valuable contribution to our knowledge. They would be still more valuable if the conclusions drawn from them as to the segmentation of the arthropod head were valid, since these afford a pretty solution of a vexing problem. For this reason it is important that these conclusions and the evidence on which they are based should be very carefully examined.

Nowhere in the previous literature on the morphology and development of the Polychaeta is there any evidence to support their interpretation of the proboscis. This they attribute to the inadequacy of earlier observations. It was no part of their intention, however, to analyze the conclusions reached by others. They were concerned only with presenting the evidence provided by a critical examination of the nervous system, and the drawing of conclusions from this evidence. In assessing the validity of their conclusions, however, it is necessary to weigh their evidence against that obtained from other sources.

In an earlier paper (DuPorte, 1953) I pointed out that, even if their basic conclusion, the metameric origin of the proboscis, is correct, it is possible to draw valid alternative conclusions as to the morphology of the insect head from the evidence presented by Henry. I shall attempt to show now that there is a reasonable doubt as to the validity of this basic conclusion.

THE PRIMITIVE POSITION OF THE MOUTH

There have been several theories of the origin of bilaterally symmetrical animals, the following being among the more prominent. (a) Transition from a ctenophore to a hypothetical "Trochozoon". (b) Transition from a ctenophore to a polyclad turbellarian. (c) Transition from a planula to an acoeloid turbellarian. (d) Development of an acoeloid turbellarian by the cellularization of a multinucleate infusorian. These theories all imply that primitive Bilateria had the mouth ventral in position and posterior to the principal nerve cell concentration.

In the Proterostomia, that branch of the Animal Kingdom to which the annulates belong, the blastopore forms the mouth or the mouth opens where the blastopore closes, therefore, the mouth must be considered to be primitively ventral in position.

The embryonic mouth in arthropods develops on the ventral side, some distance behind the apex and posterior to the protocerebrum and deutocerebrum.

Both the phylogenetic and the ontogenetic evidence suggest, therefore, that the brain and structures associated with it are morphologically preoral in bilaterally symmetrical animals. If the mouth in insects is secondarily apical the change can be accounted for in one of two ways—the forward migration of the mouth, or the loss of the prostomium coupled with a backward shift of the brain. There is no adequate evidence for either of these assumptions.

POSITION OF THE MOUTH IN THE POLYCHAETA

There is a respectable body of work on the development of the Polychaeta and, for the most part, there is essential agreement on the basic phenomena described.

Ferris (1953) believes "that it is possible to think of the Arthropoda as having developed from the Polychaeta, without worrying too much about the place and fate of the trochophore in the evolutionary series". This, of course, is true as we are no longer committed to reading phylogenetic significance into all larval structures, but the adult polychaete does develop by metamorphosis of the trochophore, and the development of segmentation during metamorphosis has been described for several species. If the proboscis consists of invaginated apical segments we should expect to find some evidence of this in the development of the larva.

The mouth in the typical trochophore lies near the middle of the ventral side, posterior to the prototroch which forms the boundary between the anterior and posterior regions. The posterior region, containing the mouth, usually becomes segmented, the most anterior intersegmental line being just in front of the mouth. Nowhere is there to be found any description of segmentation in the anterior region, but all authors agree that the prostomium and the brain develop from this region.

The mouth of the newly-hatched trochophore opens into a short tube interpreted as the stomodaeum. It is difficult to see what other interpretation can be given to this tube. If, therefore, the proboscis is formed by the invagination of three segments, these must have invaginated after hatching. Furthermore, since according to Ferris and Henry the prostomium belongs to the third segment, these invaginated segments must have developed in the anterior region of the trochophore. It might be argued that these segments are added during metamorphosis as the trunk segments are added at the posterior end, but there is not the slightest indication of any such development in the records. Where then do these segments come from?

The metamorphosis of the archiannelid *Polygordius neapolitanicus* (Fig. 1) as described by Woltereck (1905) affords conclusive proof that the prostomium in this species is preoral.

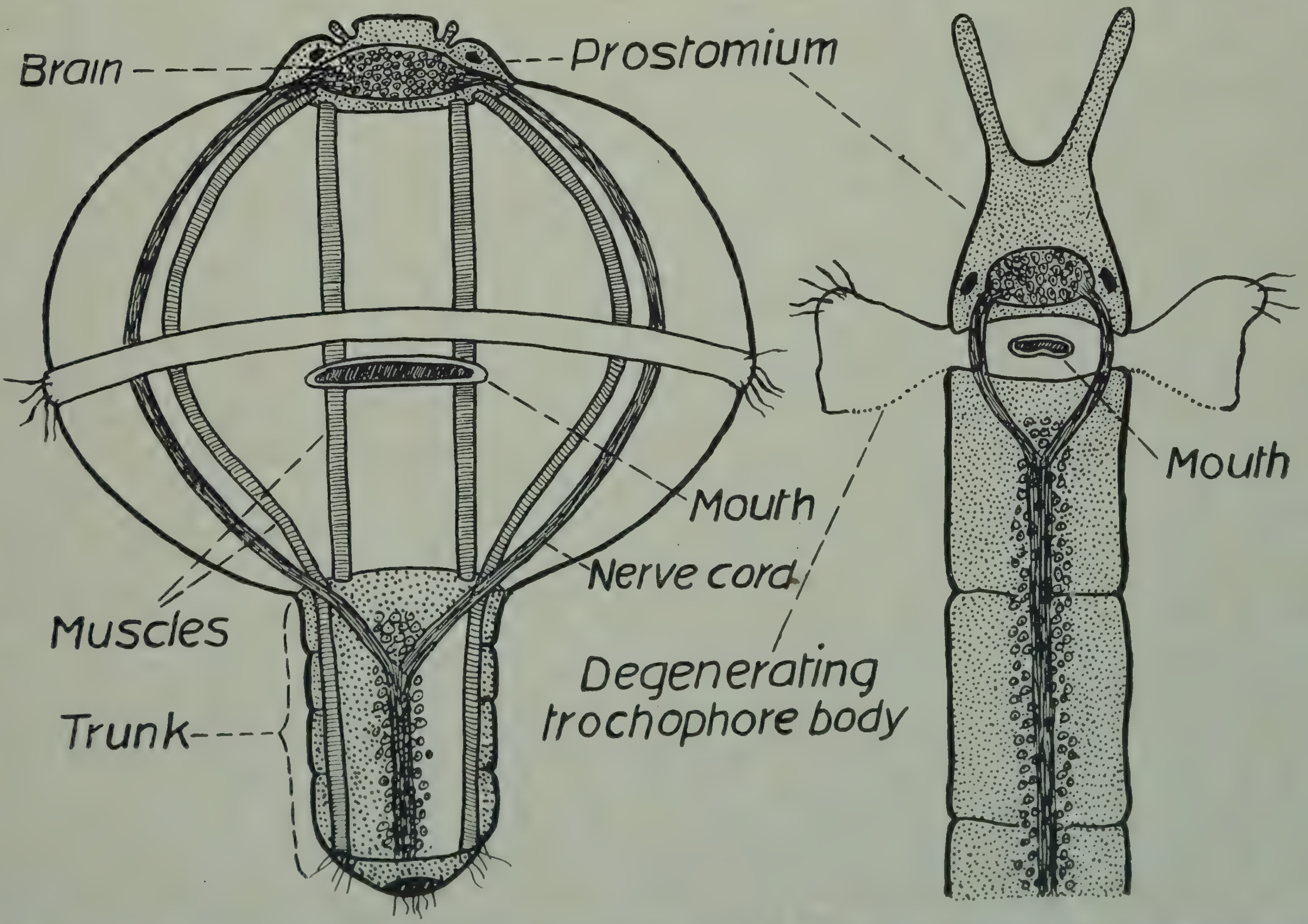

Fig. 1. Two metamorphic stages of *Polygordius neapolitanicus* showing the atrophy of the trochophore body (after Woltereck).

The prostomium, brain and prostomial sense organs develop from the apical organ of the trochophore, and the trunk segments are added to the posterior end in the typical manner. The trochophore body, apart from the apical organ, plays no part in the formation of the adult, but gradually atrophies. As it atrophies, contracting longitudinal muscles pull the apical prostomium and the trunk segments towards each other until they meet. These changes do not affect the digestive tract, and the mouth retains its position near the middle of the degenerating trochophore body. When the junction of the prostomium and the trunk is effected the mouth lies between the two. The prostomium of *Polygordius* is essentially similar to that of the Polychaeta. That it is preoral in origin and in definitive position is obvious.

Ferris (1953) categorically refuses to consider evidence such as the foregoing, asserting that "until some real evidence has been presented to show where we are wrong and must be wrong . . . we see no reason to alter our hypothesis. We would, for example, accept none of the work which has been done on the embryology of the Polychaeta, and none of the published work which we have seen on the nervous system of the Polychaeta, and none of the evidence which we have seen in regard to the 'eversible pharynx' of the Polychaeta as constituting such evidence". Undoubtedly much of the earlier work on the development and morphology of the annelids needs checking and re-assessing, and it is to be hoped that there will soon be further critical work done with Ferris' theory in mind. I cannot, however, condone this cavalier and indescriminate jettisoning of all previous work. I shall therefore attempt to present what I hope will be regarded as "real evidence", not that Ferris and Henry *are* wrong, or *must be* wrong but that the chances are at least fifty-fifty that they *may be* wrong. To do this I shall demonstrate that the nerves of the polychaete proboscis which Henry interprets as segmental nerves can, as justifiably, be interpreted as stomodaeal nerves on the available evidence.

ANALYSIS OF HENRY'S EVIDENCE

The drawings in Figure 2 are adapted from Henry (1947, 1948). They show the origins of the stomodaeal nerves and of some anterior segmental nerves as she interprets them. For better comparison with the polychaete *Nereis* the stomodaeal nerves in the other drawings are directed anteriorly, as they would be if the stomodaeum were everted.

Ferris and Henry's interpretation is, to a large extent, based on the assumption, first made by Hanström, that the stomodaeal nerves invariably arise from the most anterior ganglion of the primitive ventral chain. This is probably the prostomial ganglion in the Oligochaeta and the ventral region of the brain in the Polychaeta and Onychophora. Their assumption appears to be sound because in all annulates the stomodaeal nerves do seem to originate directly in this ganglion or else in the stomodaeal commissure which, passing beneath the stomodaeum, unites the two halves of the ganglion. The stomodaeal nerves in the Hirudinea (Hanke, 1948) and the Oligochaeta (Henry, 1947) arise from the commisure. In the Onychophora (Henry, 1948), as well as in insects and many other arthropods, the recurrent nerve, or principal stomodaeal nerve, arises from the ventral region of the brain, but other stomodaeal nerves may arise from the commissure. As far as the evidence goes, nerves arising from the commissure are always stomodaeal, never segmental. The recognition of this commissure is therefore important in determining whether certain structures or regions are stomodaeal or segmental in origin.

The stomodaeal commissure in the oligochaete *Lumbricus* (Fig. 2A, Sc) is quite distinct from the circumoesophageal connective (Cc) but is connected to it by a series of bridges. The stomodaeal nerves (R, St) arise distinctly from the commissure and not from the connective. In *Peripatoides* and in many other annulates there is a tendency for the stomodaeal commissure to unite with the circumoeosophageal connective for varying distances beyond the brain (Fig. 2B, Sc + Cc). When a nerve is given off from this common trunk it is not possible, in the absence of other conclusive evidence, to tell by topographical inspection whether it arises in the commissure or the connective. In *Peripatoides* the recurrent nerve (R) arises from the ventral region of the brain. Another stomodaeal nerve (St) arises from the common cord and presumably has its origin in the commissure.

The commissure and connective are completely and indistinguishably united in the oligochaete *Diplocardia* (Fig. 2C, Sc + Cc) except for a short distance behind the brain. Even this separation does not occur in some individuals, but at the point where separation

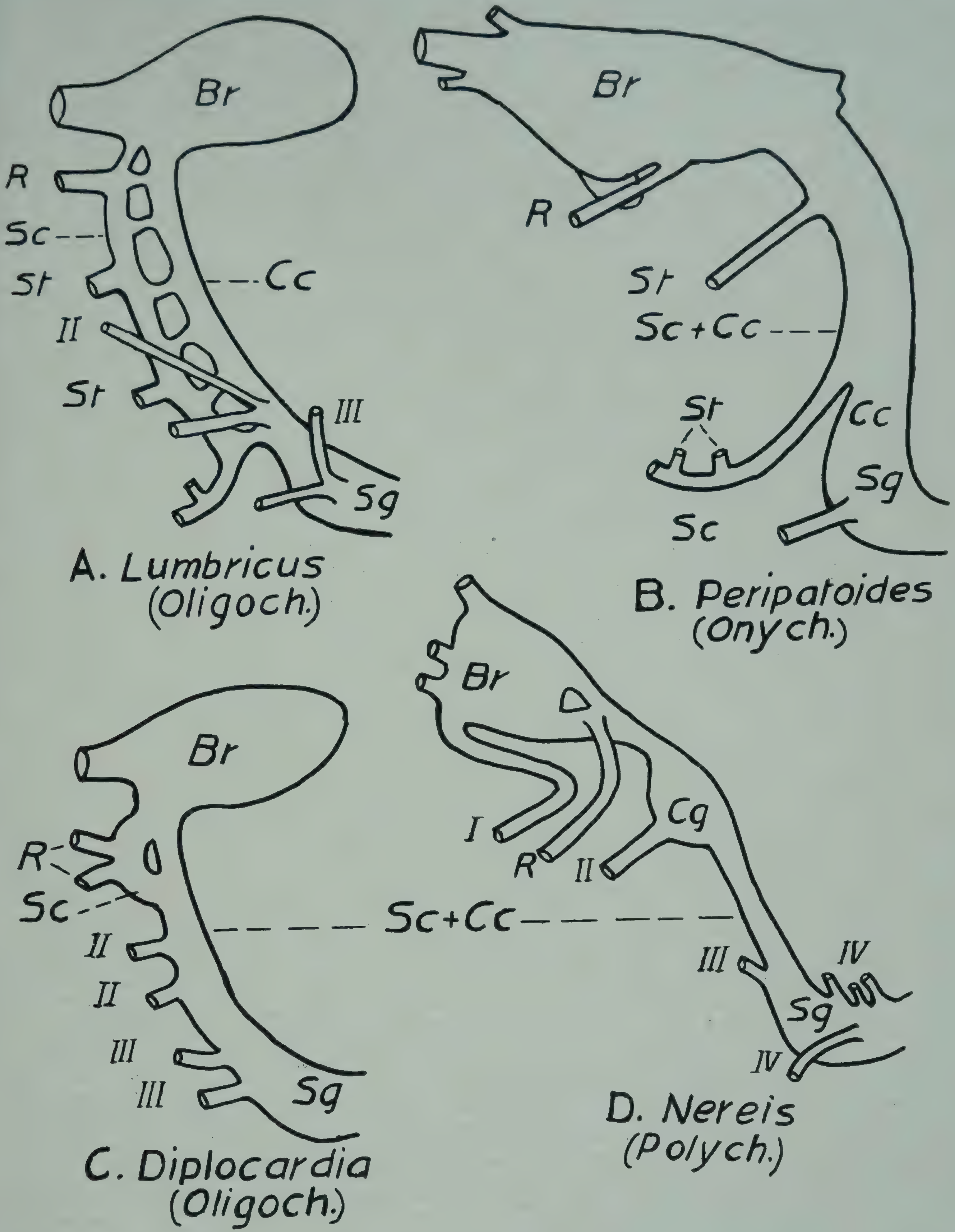
Br
R
Sc
St
II
St
Cc
III
Sg
A. Lumbricus (Oligoch.)
Br
R
St
Sc+Cc
St
Cc
Sg
Sc
B. Peripatoides (Onych.)
Br
R
Sc
II
II
III
III
Sg
Sc+Cc
C. Diplocardia (Oligoch.)
Br
I
R
II
Cg
III
IV
Sg
IV
D. Nereis (Polych.)

Fig. 2. Anterior nerves of some annulates (adapted from Henry). Br, brain; Cc, circumoesophageal commissure; Cg, connective ganglion; R, recurrent nerve; Sc, stomodaeal commissure; Sg, suboesophageal ganglion; St, stomodaeal nerves; I, II, III, IV segmental nerves as interpreted by Henry.

normally occurs there is a bilobed swelling (Sc) on the anterior side of the composite nerve cord. This has the appearance of a ganglion and its similarity to the connective ganglion of the polychaete *Nereis* (Fig. 2D, Cg) should be noted.

None of the Polychaeta illustrated by Henry has a free stomodaeal commissure. In view of the general tendency for the commissure and connective to unite we are justified in assuming that there is complete union of the two in the polychaetes. This is borne out by the fact that the circumoesophageal nerve cord arises by two roots from the brain. Henry recognizes this when she states that "it must therefore be assumed that the stomodaeal commisure, which is free in some Oligochaeta, has fused with the connective".

The semblance of segmentation is most marked in the proboscis of *Nereis virens* since transverse grooves separate the regions which, on the distribution of the nerves, Henry regards as segments. This species will therefore serve as a good example for comparison with other annulates. Henry describes and figures four pairs of nerves supplying the proboscis in *Nereis*. The first pair (Fig. 2D, I), which arises from the ventral region of the brain, she assumes to be the nerve of the first segment. The second pair (R) arises near the junction of the two roots of the composite circumoesophageal nerve cord. This she interprets as the basal portion of the recurrent or stomodaeal nerve. The two nerves on each side follow parallel courses along the side of the proboscis and terminate in a ganglion which surrounds the base of the jaw. She believes the jaws to be the persistent remnants of an obsolescent first segment innervated by the first pair of nerves. A nerve given off from each ganglion continues posteriorly along the stomodaeum and Henry regards this as a continuation of the second or "recurrent nerve". There is, in fact, no external indication as to whether it is a continuation of either nerve or whether it originates in the ganglion. It is not possible to tell either whether the first nerve is a stomodaeal or a segmental nerve. From its origin it might be either, and since it follows the same course as the second nerve, which Henry admits to be a stomodaeal nerve, and terminates in the same ganglion, it seems more reasonable to interpret it as a stomodaeal nerve arising from the ventral region of the brain as in *Peripatoides* (Fig. 2B, R).

A third nerve (Fig. 2D, II) originates in the connective ganglion, a swelling in the composite nerve cord, and innervates the oral ring. Henry interprets this as the nerve of the second segment, therefore the ganglion is presumably the second segmental ganglion; but this ganglion gives rise to three other pairs of nerves, one of which enters the podial ganglion of the peristomium (Henry's fourth segment) while the others innervate two pairs of peristomial tentacles. If we examine the corresponding nerve cord of *Diplocardia* we find an enlargement (Fig. 2C, Sc) in the same relative position as the connective ganglion in *Nereis*. A pair of nerves (R) given off from this enlargement are obviously stomodaeal nerves and are thus interpreted by Henry. In the absence of other evidence the nerve from the connective ganglion to the proboscis in *Nereis* can be interpreted as a stomodaeal nerve arising from the commissure, while those going to the peristomium may be segmental nerves arising from the connective but probably having their origin in the suboesophageal ganglion.

The fourth pair of nerves in *Nereis* (Fig. 2D, III) arises at the junction of the composite cord with the suboesophageal ganglion and innervates the maxillary ring of the proboscis, which Henry regards as the third segment. Here again it is impossible to determine the true origin of the nerve by macroscopic inspection and it could well be a stomodaeal nerve arising from the commissure.

In *Lumbricus* the nerves of the peristomium (Henry's second segment) arise from the connective a short distance in front of the suboesophageal ganglion (Fig. 2A, II) and in *Diplocardia* nerves of both this and the next segment (Fig. 2C, II, III) arise from the composite circumoesophageal cord. Henry states that "in the Oligochaeta the nerves which arise from the circumoesophageal connective are indicative of true segmentation" and that in *Nereis* "there is a clear correspondence with the conditions found in *Lumbricus*, where nerves arising from the circumoesophageal connective pass to the second and third segments respectively". But is there a "clear correspondence"? The nerves in *Lumbricus* quite clearly branch off from the connectives, their origin, of course, being in the suboesophageal ganglion. In *Nereis* they branch off from the composite nerve trunk and their origin is unknown. In *Diplocardia* both stomodaeal and segmental nerves arise from the composite nerve cord but they can be distinguished one from the other. The stomodaeal nerves go to the stomodaeum. The others can be recognized as segmental nerves because they are distributed to regions which we know to be segments by criteria other than the distribution of the nerves. To claim that the oral and maxillary rings of the proboscis are segments solely on the distribution of nerves whose origin we do not know is begging the question.

We must conclude, therefore, that Ferris and Henry have not proved that the nerves of the proboscis are segmental in origin. On the anatomical evidence they can be interpreted, with equal justification, as stomodaeal nerves, and since all other available evidence points to the stomodaeal origin of the proboscis, the balance of probabilities decidedly favours this interpretation.

An eversible stomodaeum is not unusual. It is common in the Turbellaria where it is often provided with teeth. Jägersten (1952) has shown that the larva of the archiannelid *Protodrilus* has the stomodaeum everted in the form of a ciliated funnel for trapping microplancton. Hedgpeth (1954) considers that this condition in *Protodrilus* gives some foundation for the "suspicion that the polychaete proboscis may be a paedomorphic structure, or certainly acquired after the establishment of primary segmentation".

If the polychaete proboscis is stomodaeal in origin the basis on which Ferris and Henry ascribe an apical position to the mouth in insects is invalid. The prostomium would therefore be preoral and so would its derivatives in insects, the oculoantennal region, protocerebrum and deutocerebrum. Whether the labrum is a lobe of the prostomium or is derived from the peristomium is a problem that awaits further study.

SUMMARY

1. Ferris and Henry reject the generally accepted interpretation of the polychaete proboscis as stomodaeal in origin and of the prostomium as preoral in position. They claim instead that the proboscis consists of three anterior segments and that the prostomium is a dorsal lobe of the third segment. They believe that the apical orifice of the extended proboscis is the true mouth therefore there are no preoral structures in the annelids or in their "derivatives" the arthropods.

2. Phylogenetic and ontogenetic evidence show that the primitive position of the mouth in bilaterally symmetrical animals is posterior to the principal nerve centre, and this is the position of the mouth in the embryos of arthropods.

3. Available descriptions of the development of the Polychaeta give no evidence of invaginated anterior segments. They do give direct evidence of the preoral position of the prostomium.

4. The theory of Ferris and Henry is based on the distribution of the nerves. Segmental nerves arise from neuromeres or their connectives, stomodaeal nerves from the ventral region of the brain or from the stomodaeal commissure. The nerves of the proboscis, interpreted as segmental nerves by Henry, arise from the ventral region of the brain and from the circumoesophageal nerve cord; but the latter is a composite cord formed by fusion of the stomodaeal commissure and the circumoesesophageal connective and Henry has not shown that the nerves which arise from it originate in the connective and not in the commissure. Her work therefore gives no stronger support for the segmental than for the stomodaeal origin of the proboscis.

5. The weight of evidence is therefore in favour of the preoral position of the prostomium. There is also good evidence that at least the oculo-antennal region, the protocerebrum and the deutocerebrum of insects are derived from the prostomium and are therefore preoral.

REFERENCES

DuPorte, E. Melville. 1953. The protocephalon: a critique of recent interpretations. *Canad. Ent.* 85: 41–55.

Ferris, G. F. 1942. Some observations on the head of insects. *Microentomology* 7: 25–62.

Ferris, G. F. 1953. On the comparative morphology of the Annulata. A summing up. *Microentomology* 18: 2–15.

Hanke, Ruth. 1948. The nervous system and segmentation of the head in the Hirudinea. *Microentomology* 13: 57–64.

Hanström, B. 1928. Vergleichende Anatomie des Nervensystems der wirbellosen Tiere. Berlin.

Hedgpeth, Joel W. 1954. On the phylogeny of the Pycnogonida. *Acta zool. Stockh.* 35: 193–213.

Henry, Laura M. 1947. The nervous system and the segmentation of the head in the Annulata, sections I, II, III. *Microentomology* 12: 61–110.

Henry, Laura M. 1948. The nervous system and the segmentation of the head in the Annulata, sections IV–VII. *Microentomology* 13: 1–48.

Jägerston, Gösta. 1952. Studies on the morphology, larval development and biology of *Protodrilus*. *Zool. Bidr. Uppsala* 29: 425–512.

Lankester, E. Ray. 1881. Observations and reflections on the appendages and on the nervous system of *Apus cancriformis*. *Quart. J. micr. Sci.* N.S. 21: 343–376.

Snodgrass, R. E. 1938. Evolution of the Annelida, Onychophora and Arthropoda. *Smithson. misc. Coll.* 97(6): 1–159.

Woltereck, R. 1905. Wurm "Kopf", Wurmrumpf und Trochophora. Bemerkungen zur Entwicklung und Ableitung der Anneliden. *Zool. Anz.* 28: 273–322.

The Insect Tentorium and its Antecedents

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ABSTRACT

The insect tentorium is a cuticular substitute for the non-cuticular endosternum of the Chelicerata and the intergnathal ligament of the lower Crustacea, from which arise the ventral muscles of the mouth parts. A broad intergnathal ligament is present in the chilopod Scutigera, *but it is supported by a pair of apodemes arising from two premandibular sternal plates. In* Lithobius *the ligament is a narrow bridge between the apodemes and most of the muscles are taken over by the apodemes. In Thysanura the ventral apodemes are present, but no supporting plates or connecting ligament, and an independent cuticular bar crosses the back of the head cavity. The apodemes and the bar are united in Pterygota, forming the typical tentorium. The roots of the apodemes lie close to the mesal margins of the mandibles in larval Ephemerida, in which the mandibles have no connection with the clypeus. In the higher Pterygota these roots of the anterior tentorial arms have moved into a submarginal groove of the cranium just laterad of the mandibles, and the mandibles have acquired their secondary anterior articulations on the basal angles of the clypeus. The submarginal cranial grooves are continuous with the fronto-clypeal sulcus, and in the higher insects the anterior tentorial pits have migrated in this groove to a facial position.*

Les Pleures thoraciques d'Insectes Aptérygotes et celles des Malacostracés

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C'est actuellement de Myriapodes, les Symphyles, ou plutôt, d'hypothétiques "Protosymphyles" que l'on fait dériver directement les Insectes (Snodgrass, 1938, p. 148); il n'est plus question de Crustacés. Il reste cependant que des caractères plus ou moins "crustacéens" s'observent chez certains Aptérygotes, les Machilides. Ainsi, leur mandibule dont Hansen (1893) a montré la curieuse ressemblance avec celle de *Diastylis*, un Cumacé; le style coxal des pattes thoraciques en lequel on a vu l'exopode d'une patte biramée; la volumineuse musculature abdominale dont l'un de nous (Barlet, 1946, p. 78) a montré l'allure générale: ses torsades rappellent celles qui occupent l'abdomen d'un Malacostracé, une *Mysis* p.ex.

Le style coxal des Machilides ne peut évidemment être un exopode que si l'article qui le porte est l'homologue du basipodite des Crustacés. Cette dernière opinion a été défendue avec insistance par Hansen (1893, 1925). Divers auteurs, p.ex. Vandel (1949), l'ont considérée comme dûment démontrée. Snodgrass (1927) ne l'a pourtant pas admise. En une coxa d'Insecte, il ne voit rien d'autre qu'un coxopodite, le précoxopodite des Crustacés occupant alors le niveau de la "subcoxa" ou pleuron de l'Insecte.

Dernièrement, nous avons étendu aux Crustacés Malacostracés les recherches sur la morphologie de la base du membre que nous avons longtemps limitées aux Insectes. Les résultats ainsi obtenus feront l'objet d'un mémoire détaillé et illustré. Nous nous bornerons ici à de brèves indications.

Ainsi que Hansen et Snodgrass, nous avons adopté comme base de comparaison le maxillipède d'*Anaspides tasmaniae*[1], une forme de Malacostracé que l'on s'accorde à considérer comme particulièrement "primitive". Nous avons trouvé que Snodgrass n'y a pas correctement situé le coxopodite. Ce dernier n'est pas l'article proximal qu'il a figuré (1952, fig. 38, C) porteur de deux endites et de deux exites, mais un anneau très court intercalé entre le dit article et le basipodite. L'anneau avait été interprété antérieurement par Hansen (1925, Pl. V, fig. 3 e) comme basipodite, parce que c'était de lui que paraissait dépendre l'exopode.

Or, celui-ci appartient au "préischiopodite" de Hansen qui est, selon Snodgrass, le basipodite ou homologue du trochanter.

Le soi-disant coxopodite de Snodgrass chez *Anaspides* doit correspondre au pleuron d'Insecte. Nous y avons trouvé intérieurement un processus "pleural" assez court mais enveloppé d'un "fourreau" rappelant la gaine du long processus des Machilides (Carpentier, 1946, fig. 6, p. 175). L'endosternite dont dépend le "fourreau" est, comme celui des Aptérygotes, sous-hypodermique, relié seulement à la basale de l'hypoderme. Une différence importante est que, chez les Insectes—aussi bien Ptérygotes qu'Aptérygotes—le nerf crural est antérieur à l'apophyse furcale ou à son équivalent sous-hypodermique, alors que, chez *Anaspides*, le nerf en question passe en arrière du même lieu morphologique. Nous avons trouvé le nerf crural postérieur également chez des Malacostracés Décapodes (*Penaeus* et *Amalopenaeus*) qui possèdent, eux, des apophyses "furcales" cuticulaires. Force nous est de remettre à plus tard la discussion de ces faits.

De toute façon, le précoxopodite d'*Anaspides* semble ne pouvoir correspondre qu'à un pleuron. En tout ou en partie: peut-être est-ce tout le pleuron, notre anapleure donc aussi bien que notre catapleure, le processus d'*Anaspides* se situant un peu plus bas que la marge supérieure du précoxopodite. Peut-être aussi notre anapleure est-elle représentée à la base du maxillipède d'*Anaspides* par une région plus proximale que le précoxopodite et que Snodgrass (1952, p. 134) a qualifiée de "latérotergale". Nous n'oserions en décider, notre matériel ne nous ayant permis qu'une étude incomplète de la musculature.

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[1] Matériel procuré par M. Percival (Christchurch, Nouv.-Zélande) par l'obligeant intermédiaire de M. le Prof. H. Damas (Liège).

BIBLIOGRAPHIE

Barlet, J. 1946. Remarques sur la musculature thoracique des Machilides (Insectes, Thysanoures). *Ann. Soc. Scient., Bruxelles*, série 2, 60: 77–84.

Carpentier, F. 1946. Sur la valeur morphologique des pleurites du thorax des Machilides (Thysanoures). *Bull. Ann. Soc. ent. Belg.* 82: 165–181.

Hansen, H. J. 1893. Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insecten. *Zool. Anz.* 16: 193–198, 201–212.

Hansen, H. J. 1925. Studies on Arthropoda, 2. Copenhagen.

Hansen, H. J. 1930. Studies on Arthropoda, 3. Copenhagen.

Snodgrass, R. E. 1927. Morphology and mechanism of insect thorax. *Smiths. Misc. Coll.* 80.

Snodgrass, R. E. 1938. Evolution of the Annelida, Onychophora and Arthropoda. *Smiths. Misc. Coll.* 87.

Snodgrass, R. E. 1952. A textbook of arthropod anatomy. Ithaca, N. Y.

Vandel, 1949. *In* Grassé, Traité de Zoologie, Vol. 6. Paris.

Ressemblances entre les Pleurites et Sternites thoraciques de Thysanoures et ceux de Ptérygotes inférieurs

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Il a été dernièrement démontré (Carpentier, 1955) que les trois arcs précoxaux possédés par les Lépismes—anapleurite, catapleurite et trochantin—se retrouvent fort reconnaissables chez un Ptérygote relativement inférieur, une Blatte. Le "latéropleurite" d'une Blatte et son anépisterne appartiennent à l'arc anapleural et celui-ci se prolonge dans le district épiméral du segment. Son "latérosternite" (La Greca, 1949) appartient à l'arc catapleural. Celui-ci se continue en direction de l'apodème pleural, par-dessus le trochantin, en catépisterne; mais l'angle supérieur du trochantin très développé a presque interrompu cette continuation, de sorte que les auteurs n'ont pas remarqué que les deux sclérites appartiennent au même arc primitif.

Des restes d'arc se retrouvent également dans les flancs du thorax d'un Orthoptère sauteur tel que *Tettigonia*. Un trochantin et un "latérosternite" catapleural sont bien reconnaissables. A l'angle supérieur du trochantin, l'arc catapleural est pratiquement interrompu, comme chez la Blatte; il reprend, en direction de l'apodème pleural, sous forme d'une bandelette catépisternale. La catapleure est donc relativement peu développée. Le "latéropleurite" n'est pas sclérifié, mais le restant de l'anapleure s'est élevé en une haute plaque qui forme la quasi totalité du pleuron méso- ou métathoracique de la Sauterelle[1].

Les sternites thoraciques de certains genres de Sauterelles ont développé au-dehors une paire d'épines coniques ou foliacées. Les expansions foliacées, chez certaines espèces, adhèrent l'une à l'autre le long de la ligne médioventrale. On sait, d'autre part, qu'une plaque sous-sternale existe chez de nombreux Lépismatides. Et, en certains cas, ces plaques semblent doubles comme si elles résultaient d'une unification secondaire d'une paire d'expansions. Il sera, croyons-nous, fructueux de préciser autant que possible les termes de la comparaison qui nous est ainsi suggérée: depuis que Ferris (1940) a exprimé des idées nouvelles quant au sternite des Insectes, rien de ce qui peut éclairer l'histoire de cette région ne saurait être considéré comme négligeable.

BIBLIOGRAPHIE

Carpentier, F. 1955. Pleurites thoraciques de Lépisme et pleurites de Blatte. *Bull. Ann. Soc. ent. Belg.* 91: 220–226.
Ferris, G. F. 1940. The myth of the thoracic sternites of insects. *Microent.* 5: 87–90.
La Greca, M. 1949. L'evoluzione delle pleure pterotoraciche degli Insetti Blattotteroidi. *Boll. di Zool.* 16: 119–129.

DISCUSSION

M. S. Ghilarov. Je pense que l'homologie des parties différentes des extrémités des Crustacés et des Insectes est très douteuse, parce que ce sont des groupes très éloignés. La ressemblance des parties différentes des extrémités dans ces groupes, peut aussi être considérée comme le résultat de convergences; l'évolution des extrémités articulées chez différents Arthropodes subit les mêmes régularités. Je dois encore attirer l'attention sur le fait que, selon les études du morphologiste russe E. Becker, à Moscou (1928), dans le cours d'évolution des insectes l'enclavement des pleurites se placerait à l'extrémité.

Il est prouvé par des données sur leur morphologie, leur embryologie et surtout leur écologie comparée que les Thysanures sont très proches des Ptérygotes.

A mon avis, tel que je l'ai publié en 1949, les Thysanures composent un groupe d Aptérygotes voisin des Ptérygotes. Les études sur l'embryologie et le développement postembryonique de *Lepisma saccharina* faites par A. G. Sharov, ont prouvé que le développement des Thysanures est très ressemblable à celui des Ephémérides. L'opinion de A. Handlirsch sur le caractère dégradé des Thysanures, n'a aucune base morphologique ou écologique; mais Handlirsch avait raison de les placer parmi les Ptérygotes.

C. Delamare Deboutteville. La ressemblance entre les pleures de Syncarides (Barlet) et des Ptérygotes peut porter sur des convergences. Le Crustacé Nauplien (*Mystacocarida*) ne présente rien de tel.

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[1] Au prothorax existe une condition secondaire, la cryptopleurie.

Relationships of Protura

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When I accepted the invitation of our worthy chairman to make clear to myself and if possible to you what I thought about the relationships of Protura to other Arthropods I had not seen the unqualified statement by the *Altmeister* of insect morphology, Dr. Snodgrass, which runs: "Here, surely, is a collection of diversely distributed characters sufficient to disconcert the most expert phylogenist". I was disconcerted myself already before I knew that even expert phylogenists would be, and I am so still; I feel able only to give some statements in connexion with a comment on the essential characters, but not to give a hypothesis, much less a solution.

If we have to rank a group among other groups the decision depends on the value given to each of the characters. Hennig in a recent paper (1953) has tried to direct this decision by introducing some terms which in fact do not introduce anything new, but which may help to clear up the mind and to avoid confusion. He calls primitive characters plesiomorph and derived characters apomorph; the aim of the phylogenist then is to find synapomorphs and to rule out symplesiomorphs, i.e. to find those characters common for two or more groups that are derived and rule out those that are only common inheritance. Though these indeed are commonplace thoughts they prove valuable to bear in mind. On another point I cannot follow Hennig, namely when he states that as long as a convergence is not proved we should reckon with relationships; convergence, I fear, is a much more common feature than generally supposed; I have often had to include this in my considerations.

A great many characters show with certainty that the ectognathous Thysanura with the Pterygota form a group distinctly opposed to the three entognathous groups: the ectognathous mouthparts, the building of the mandible and labium, the tentorium, the compound eyes, the annulated antennae, the shape of the external genitalia, three- to many-jointed tarsi, the shape of the tracheal system, are all characters distinctly different from those of the three entognathous groups. But do these three groups in reality form one group or not?

That the mouthparts are entognathous must mean that the sides of the cranium overgrow the underside of the head. It is generally supposed that the head originally was hypognathous and that prognathy is a derived condition caused by the expansion backwards of the postgenal areas of the cranium, in which way the mouthparts are pushed forward. But the postgenal areas may be prolonged also so to say forwards and thus form prognathy without pushing the mouthparts forward. This is, I think, what has happened to the entognathous insects. The figure, very roughly drawn, may illustrate what I mean. Of course this *may* happen more than once during phylogeny, but will it probably do so?

The sides of the cranium may fuse on the underside, thus extinguishing the proximal part of the labium. This has happened in Protura and Collembola where only a short triangular piece with the palpi is left. Or they may not fuse on the underside, thus allowing for a broad proximal part of labium. This happened in Diplura. In all cases, however, some accretion took place around the bases of the mandibles and the maxillae, resulting in the pouches of these mouthparts.

In the walls of these pouches arose some sclerotizations—"to" shore them up or just because the cuticle thickened in these folds. This is the origin of the small rod from the base of the mandible to the head wall in Collembola and Protura; perhaps the same rod in Chilopoda has a parallel origin, but homologous they need not be. This is also the origin of the so-called tentorium in the three groups which Snodgrass for Collembola and Diplura and I for Protura have shown to be sclerotizations in the ventral wall of the head, i.e. remnants of the primary sternal sclerites of the head segments giving rise to the hypopharynx. In Amphipoda and Isopoda and other Crustacea similar sclerotizations of the ventral wall of the head occur, in a similar manner and supporting the maxillae etc., but again I think we have to do with convergence. The "tentoria" of entognathous insects certainly do not prove a relationship with Crustacea.

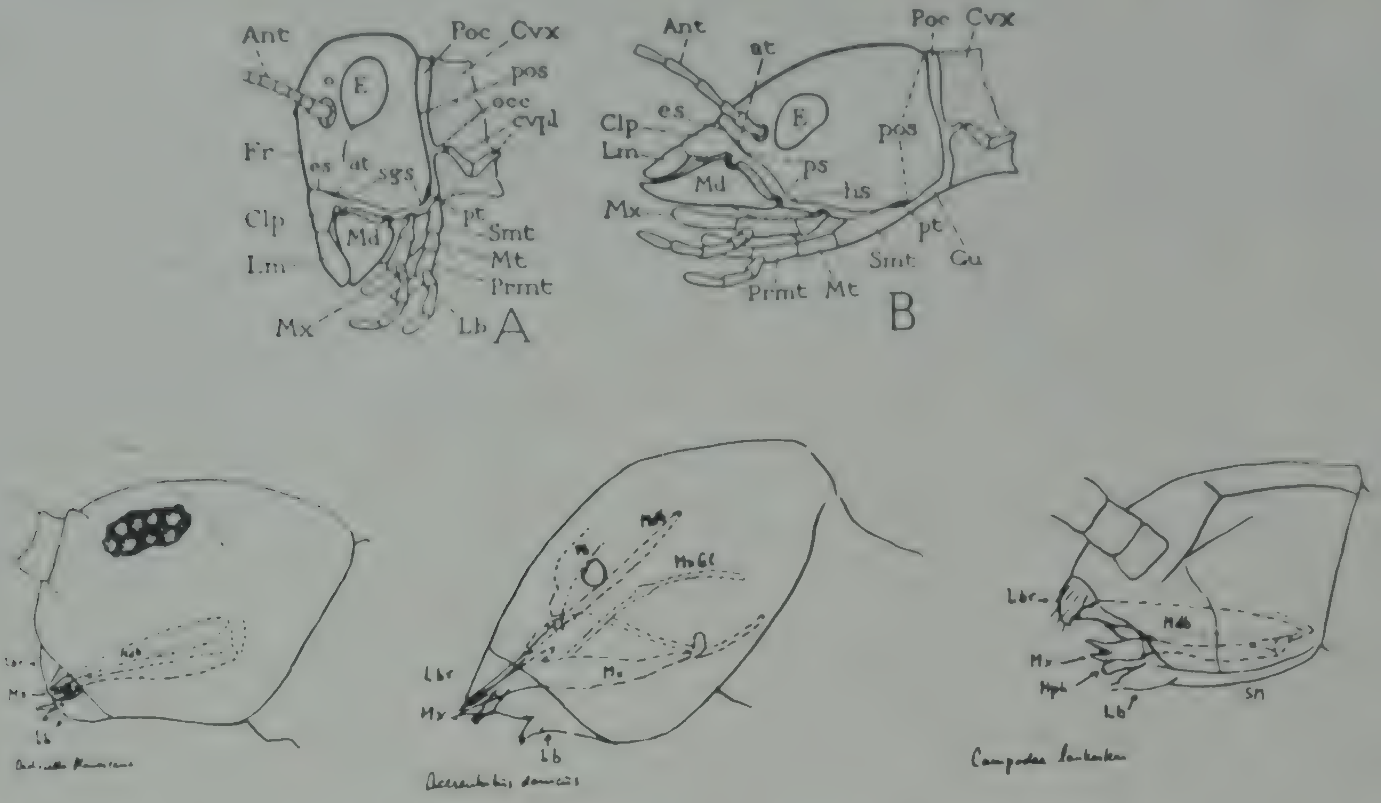

Fig. 1. Above: A hypognathous and a prognathous insect (after Snodgrass 1935). Below: Rough sketches of the head of a Collembolan (*Orchesella flavescens*), a Proturan (*Acerentulus danicus*), and a Dipluran (*Campodea lankesteri*).

The mandibles are of the one-condylized type in Entognatha. So is also the *Machilis* mandible, mandibles of Lepismatids and Pterygota having two condyles. In fact the mandibles in Protura and Diplura have no condyles at all, terminating in an acute angle in the pouch. They are undivided in contrast to Myriapods except Pauropoda, and are of a very simple shape with a split at the tip.

The maxillae in Entognatha consist of a cardo, hinged to the sternal head sclerotization, a stipes which is open interiorly, and an apical part which in Collembola is simple, whereas in Protura and Diplura a galea, lacinia and a palp are recognizable. They are of the insectan type suggestive of Symphylan maxillae, but of no other Myriapod maxillae. The maxillary glands are very much like those in Pauropoda (Tiegs 1947), but I have not found their like in other Entognatha.

The hypopharynx seems to be quite absent in Protura; in Collembola and Diplura it is well developed, suggestive of a Symphylan and a primitive ectognathan hypopharynx.

The Protura have no eyes nor antennae. These certainly are derived characters and do not prove any relationship. I think the pseudoculi are remnants of the antennae; but they have also been considered homologous with the postantennal organs of Collembola and the Tömösvary organ of Myriapods, and this, of course, would prove some relationship to Collembola and Myriapoda as this organ is not found elsewhere.

The foretarsi in Protura have taken over the function of the missing antennae, being equipped with numerous sensillae, but this also is a derived character and proves nothing.

The leg consists of coxa, trochanter, femur, tibia, tarsus, and praetarsus with one claw and a so-called empodial appendage. This appendage is certainly not another claw. The same condition is present in Collembola; even the "wings" of the Collembolan claw may be encountered in the second and third legs of Protura; the character may be primitive and a fore-runner of the two-clawed condition with empodium in Pterygota. The Myriapoda with one-clawed praetarsus do not seem to have an empodial appendage.

In the pleurum of Protura some sclerites are described as representing subcoxa and even trochantin. They are distinct, but the leg nature is dubious. In Collembola an independent subcoxa is sometimes found, in Diplura conditions are more like Protura.

In all Entognatha there are distinctly three pairs of thoracic legs and three distinct thoracic segments.

A Y-shaped sternal apodeme on meso- and metasternum is present alike in Protura and *Japyx*, but to my knowledge not in Collembola nor other Arthropods.

The abdomen of Protura consists of 12 segments, the last being the telson surrounding the anus and with distinct dorsal and ventral sclerites. This condition is found in some insect embryos, but not in any other adult insect. It is certainly a primitive insectan character. Ectognathous *Lepisma* embryos have 12-segmented abdomen, Dipluran embryos only 11-segmented (10-segmented as adults) and Collembola 6-segmented. Cerci are wanting in Protura and Collembola, present in Diplura. Three pairs of abdominal legs are present in Protura, but more seem to have been present in earlier time, so to say becoming incorporated in the sterna of the following segments as indicated by the number of setae in the sterna of the first three abdominal segments and the following ones. Abdominal legs are a primitive character common to Arthropods.

Two large abdominal glands open on the eighth abdominal segment below the tergal comb; I do not know of any homologues in Arthropoda.

The outer genitalia as they are developed in Ectognatha and Pterygota do not occur in Entognatha, not even a sclerotic penis, the penis described by Silvestri in *Centrjapyx* being dubious. In some Chilopods a pair of gonopods are present, in progoneate Myriapods other conditions prevail. The question opisthogoneate versus progoneate has lost its overwhelming importance after Tiegs (1949) proved that the progoneate exit ducts develop in quite another way than the opisthogoneate ones, which is the primitive condition.

The Protura have developed an external copulatory apparatus quite of their own, comparable to that of no other group. They were with no right compared with the cerci by Handlirsch because they open between the 11th and 12th abdominal segments in both sexes. They are innervated from the last abdominal ganglion which by Berlese is said to comprise ganglia from abd. VI–VIII, but it does not follow that they belong to the eighth abdominal segment, the nervous system being too little developed. Nor do I understand the statement by Imms (1936), that "the extension of anamorphosis has resulted in the backward migration of the gonopore", because in anamorphosis the new segments are intercalated anterior to the telson, and so also in Protura, not anterior to the gonopore segment. The opening of the gonopore behind segm. XI may be a primitive character in common with Chilopoda, or it may be a specially derived character as are the copulatory organs.

The family Eosentomidae has two spiracles, on meso- and metathorax latero-dorsally. In Collembola some highly developed species have a head-spiracle as have the Symphyla (but in another location), the Scutigera have median dorsal spiracles, the Diplopods have immediately near each leg base a bundle of tracheae in an apodeme; only the Diplura have a tracheal system approaching that of Ectognatha and Pterygota. In meso- and metathorax both latero-dorsal and latero-ventral spiracles are present in Japygidae, the latero-ventral spiracles being comparable to those of the Pterygotan thorax whereas the Pterygotan abdomen has latero-dorsal spiracles. The latero-dorsal thoracic spiracles are homologous with those of Protura. I should think, therefore, that the tracheal system is polyphyletic, those of Symphyla, Collembola, Diplopoda and Scutigera being of different origin to that of Ectognatha-Pterygota which has its origin in Diplura-Protura, comparable perhaps with that of *Lithobius*, where most segments have latero-dorsal spiracles and no segment latero-ventral spiracles. The tracheal system in Protura thus may be primitive, showing relation to Diplura and perhaps to Chilopoda. In Pauropoda a tracheal system is missing.

The Malpighian tubules in Protura are of a very primitive type, six being present, but solid, not tubulous. Perhaps the six short ones described by Silvestri 1905 in *Anajapyx* are alike. Malpighian tubes are wanting in Collembola.

The embryonic development of Protura is unknown. In the other Entognatha the cleavage is total in Collembola as in Myriapoda and Crustacea, later superficial; in Diplura as in Ectognatha-Pterygota it is superficial. The organ described by Tiegs as "Dorsal organ" and later designated as Tiegs' organ by Remington, is known from Symphyla, Collembola and Diplura and from no other Arthropods. The total cleavage is a primitive character.

The postembryonic development is anamorphic in Protura as in most Myriapoda, but in contrast to all other insects. It is even characterized by a praelarva, with distinct embryonic characters (mouthparts, foretarsus, abdominal legs); the whole animal looks as if it could not move. In *Japyx* (Silvestri 1948) two similar stages are described, being superintended by the mother; in Pauropods and Diplopods a resting "pupoid" stage occurs immediately when the young larva hatches. No such stage is known in Symphyla, in Collembola or in other insects, yet the stage known as pseudofoetus (Verhoeff 1911) in *Machilis* may be a parallel.

Ecdyses after sexual ripeness is known in Collembola, Diplura and ectognathous Thysanura, as well as some few Pterygota. It may occur also in Protura, as the way in which I studied their postembryonal development (1949) was not suited to find this out. This is also a primitive character, as are the anamorphosis and the praelarval "pupoid" stage.

Ecdysis in Protura takes place through a transverse split at the hind border of the head as in Myriapoda and Collembola; in Diplura as in Pterygota through a Y-shaped epicranial "suture" (personal communication from Dr. Orelli, Basel).

Now we shall try to sum up. The Ectognatha-Pterygota are in many characters distinct from the three orders of Entognatha. The latter have only the entognathy and the so-called tentorium caused by this as a synapomorph character, their other mutual characters are shared with one or more Myriapod groups or they connect Myriapoda with insects.

The Protura are very specialized in many respects. The lack of hypopharynx, antennae, eyes, and cerci, the special shape of the foretarsus, the presence of abdominal glands, and the shape of the external genitalia are all special characters without phylogenetic value.

In common with Collembola they have the shape of the claw and empodial appendage; this is shared with no other group, but is certainly a primitive character leading to the leg commonly found in insects and Myriapods.

The presence of abdominal appendages is a character of reduction, thus leading from Myriapods to insects. The shape of the mandible leads from Pauropoda to insects, the shape of the maxilla from Symphyla to insects, though the shape of the maxillary gland is Pauropodan. The manner of moulting is Myriapodan, but is shared with Collembola.

Finally a set of characters combine the Protura with Myriapods and with Insecta via Diplura—the 12-segmented abdomen, the Malpighian tubes, the anamorphosis, the presence of a praelarva. The embryonic development is unknown, but probably belongs to this set of characters.

It has been said that the existence of three pairs of thoracal legs is the only character which makes the Entognatha Insecta. Maybe it is, but even then it is such an important character that it justifies itself. The concept of an insect is quite a clear-cut thing, and subtle phylogenetic speculations should not bring us away from it. After all, the distinction between Myriapoda and Insecta is a purely practical matter, and I do not see the point of including Myriapoda within Insecta, as proposed by Remington 1954, though of course it should be convenient to have the Myriapoda treated in entomological textbooks. But apart from this the concept of an insect is an Arthropod with a distinct three-segmented thorax with or without legs, and let it be so.

The Protura stand near the bottom of the real insects. Via the number of abdominal segments, the tracheal system, the Malpighian tubes, the anamorphosis, the resting (?) praelarva, and the manner of moulting they lead to the Ectognatha-Pterygota via Diplura. They are related, but not very closely, to the Collembola. They show distinct relations to the Myriapoda through the anamorphosis and the manner of moulting, to the Pauropoda through the shape of the mandible and the maxillary glands, and to the Symphyla through the shape of the maxilla; but they are not directly related to any of them.

They are insects with many characters, mostly primitive ones, in common with Myriapoda, with the entognathy as a derived character in common with Collembola and Diplura; and with most characters, both primitive and derived ones, in common with Diplura, through which group they lead to Ectognatha and Pterygota.

This is not a theory, but a mere statement of facts; it points to the near relationship of Insecta to Myriapoda in general, though not to any recent group in special, and leaves a near relationship with Crustacea out of consideration. It gives no room for a new phylogenetic tree in the holy grove of phylogeneticists, as a Dane has put it many years ago; in fact I think that the statement of relationship is a more profitable occupation than the pedigree speculations without palaeontological foundation.

REFERENCES

Berlese, A. 1909. Monografia dei Myrientomata. *Redia* 6: 1–182.

Bitsch, J. 1952. Recherches anatomiques sur le labium des Diploures. *Publ. Univ. Dijon* (N.S.) 9: 5–26.

Ewing, H. E. 1928. The legs and leg-bearing segments of some primitive arthropod groups, with notes on leg-segmentation in the Arachnida. *Smiths. Misc. Coll.* 80(11): 41 pp.

Ewing, H. E. 1942. The origin and classification of the Apterygota. *Proc. Ent. Soc. Wash.* 44: 75-98.

Hennig, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. *Beitr. z. Ent.* 3, Sonderheft, 85 pp.
Hennig, W. 1953. Meinungsverschiedenheiten über das System der niederen Insekten. *Zool. Anz.* 155: 21–30.
Henriksen, K. L. 1932. The manner of moulting in insects. *Not. Ent.* 11: 103–27.
Imms, A. D. 1936. The ancestry of insects. *Trans. Soc. Brit. Ent.* 3: 1–32.
Paclt, J. 1954. Zum phylogenetischen System der niederen Insekten. *Zool. Anz.* 153: 275–81.
Remington, C. L. 1954. The "Apterygota". *In:* A Century of Progress in the Natural Sciences: 495–505.
Sharov, A. G. 1953. Razvitie schtschetinochvostok (Thysanura Apterygota) v svjazi s problemoj filogenii nasekomych. *Trudy Inst. Morf. Živothych Moskva* 8: 63–127.
Silvestri, F. 1905. Nuova contribuzione alla conoscenza dell'Anajapyx vesiculosus Silv. *Ann. R. Scuola Sup. Agric. Portici* 6: 1–15.
Silvestri, F. 1948. Japyginae della fauna italiana finora note. *Boll. Lab. Ent. Agr. Portici* 8: 236–96.
Silvestri, F. 1949. Contributo alla conoscenza degli Japygidae. *Rend. Acad. dei Quaranta* (3) 27: 3–115.
Snodgrass, R. E. 1935. Principles of insect morphology. New York.
Snodgrass, R. E. 1947. The insect cranium and the "epicranial suture". *Smiths. Misc. Coll.* 107(7): 52 pp.
Snodgrass, R. E. 1950. Comparative studies on the jaws of mandibulate arthropods. ibid. 116(1): 85 pp.
Snodgrass, R. E. 1951. Comparative studies on the head of mandibulate arthropods. Ithaca, N.Y.
Snodgrass, R. E. 1952. A textbook of arthropod anatomy. Ithaca, N.Y.
Tiegs, O. W. 1947. The development and affinities of the Pauropoda. *Quart. J. Micr. Sci.* 88: 165–336.
Tiegs, O. W. 1949. The problem of the origin of insects. *Austr. and N. Z. Ass. Adv. Sci.*, Section D: 47–56.
Tillyard, R. J. 1930. The evolution of the class Insecta. *Pap. Proc. R. Soc. Tasmania*: 89 pp.
Tuxen, S. L. 1949. Über den Lebenszyklus und die postembryonale Entwicklung zweier dänischer Proturengattungen. *Kgl. Da. Vid. Selsk. Biol. Skr.* VI 3: 50 pp.
Tuxen, S. L. 1952. Über das sogenannte Tentorium der Proturen. *Trans. Ninth Int. Congr. Ent.* 1: 143–46.
Verhoeff, K. W. 1911. Über Felsenspringer, Machiloidea. 5. *Zool. Anz.* 38: 254–63.

DISCUSSION

M. S. Ghilarov. From the view-point of their development the Protura are in no more close relation to insects than to the myriapods.

The uniting of the Proturans and true insects in one class of Insecta is quite artificial, three pairs of thoracic legs being almost the only common character. But the development of three pairs of anterior locomotory extremities in different groups of Apterygota and ancestors of Pterygota may be regarded as the result of convergence too, as a result of adaptation to locomotion in the soil of such long, articulated and many-legged Arthropods, as Myriapods are and the ancestor of Insects probably were. The experiments with the amputation of various pairs of legs in Geophilids proved that the anterior three pairs of legs are of greatest importance for their locomotion in the soil.

The conclusions of Dr. Tuxen are very similar to my own and everybody knows, we always appreciate the data, which are in accordance with our opinion—as correct ones!

Die systematische Stellung der Collembolen

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ABSTRACT

The problem of the systematic position of the Collembola and the Apterygota has always been discussed in connection with that of the Pterygota. Two opinions, diametrally opposite, have resulted from the discussion. Tillyard, on the basis of Rhyniella cursor *from the Devonian Rhynabeds in Scotland and the protomorphosis of the Collembola regards the group as primitive, ancestral, leading from his hypothetical basic Ptotaptera to the Thysanura and from there to the Pterygota. Handlirsch, on the basis of his Trilobite-theory, states that they are young of origin and secondarily reduced and that they have at any rate no connection with the higher insects.*

In both views there is certainly a good deal of truth, but both Tillyard and Handlirsch regard the Apterygota only in relation to the evolution of the higher classes of Hexapoda and not in connection with the lower classes of arthropoda in general.

Recent research, undertaken by myself and my pupils Lindenmann (Collembola), *viz., Orelli* (Campodea), *Gyger* (Japyx), *Schäfer* (Lepismachilis), *and Sweetman* (Lepisma) *clearly show hitherto neglected differences between the Apterygota and Pterygota, so that we have to regard the former as a special Order of the Arthropoda as for example the Crustacea or Arachnids.*

To the apparent differences in morphology and embryology are added these of the postembryonic growth and behaviour, which are fundamentally different from the Insects. After a certain number of larval moults the animals reach sexual maturity, copulate and lay their eggs and then die. Collembola and all other "Apterygota" behave in this way like Crustacea. When reaching maturity moulting and copulations are going on in a special rythm. Comparing the higher and lower orders of Arthropods it is evident that the apparent hexapody of the thorax is the only link between the Apterygota and Pterygota, whilst there is much more likeness between the former and the Arachnomorpha and Crustacea. It is therefore proposed to regard them as a special order of the Arthropoda and not merely as a suborder of the Insecta.

In den Hand- und Lehrbüchern der Entomologie und Zoologie (Kückenthal, Grassé, Imms, etc.) finden wir stets Apterygoten und Pterygoten zur Klasse der Hexapoda oder Insecta vereinigt. Diese Vereinigung ist aber heute stets mit Zweifeln verbunden. Beginnt die Entwicklung der Insekten bei den Apterygoten, d.h. sind diese wirlich als vermeintliche Urinsekten tatsächlich primitiv und bilden sie den Ausgangspunkt für die pterygoten Formen oder stellen sie sekundär reduzierte Formen dar, welche erst in jüngerer Zeit entstanden sind—dürfen wir sie mit den eigentlichen Hexapoden vereinigen oder stellen sie eine eigene Entwicklungsform dar, welche mit den Pterygoten nichts zu tun hat? Dies sind Fragen, auf welche uns die heutigen Lehrbücher keine Antwort geben.

Zum ersten Male habe ich 1953 versucht das Problem schüchtern anzugreifen. Gestützt auf postembryonale Entwicklungsvorgänge bei den Collembolen habe ich die Ansicht vertreten, dass sie im Sinne der Protomorpha von Tillyard den Crustaceen parallelgestellt werden sollten und dass eine Vereinigung mit den Hexapoden nur zufällig und unnatürlich sei. 1953 hat Remington unabhängig das Problem aufgegriffen. Er kommt im wesentlichen zu den gleichen Resultaten. Die Apterygoten sind kein einheitlicher Stamm, ihre Affinitäten wie sie durch die vielen Untersuchungen an Vertretern der verschiedenen, den Symphylen Pauropoden, Collembolen und Thysanuren zugestellten Arten durchgeführt wurden, führen sie aus dem Bereiche der Hexapoden heraus. Sie erfahren also im weitesten Sinne das nämliche Schicksal, die seinerzeit die alten Aptera erfahren haben, zur denen alles was im Insektenreiche flügellos war, gerechnet wurde.

Besonders die letzten grossen Diskussionen zwischen Tillyard (1931) und Handlirsch (1937) um die Ableitung der Pterygoten waren es, welche mich auf den Weg dieser Untersuchungen führten. Bei beiden galten die Apterygoten im weitesten Sinne als zu den Insekten gehörig.

Handlirsch (1908, 1925, 1930) waren allerdings die Apterygoten etwas unbequem. Da er von der Kentniss der fossilen Insekten ausging und darin die phylogenetisch wichtigste Grundlage für eine Ableitung der pterygoten Insekten sah, so konnte er zunächst (1908) die erst seit 1925 aus dem oligocaenen Bernstein bekannten kleinen Collembolen übergehen. Er sieht in ihnen fossil junge Formen von extremer Spezialisation, die eine retrograde Entwicklung eingeschlagen haben und die im Larvenstadium, also neoten, reif geworden sind. Er spricht aber von einer möglichen Bindung mit den progoneaten Myriopoden und durch die Bildung der Antennen möglicherweise mit den Crustaceen, besonders wenn auch die 6-Zahl der Segmente nicht als primär sondern als abgeleitet betrachtete. Handlirsch (1937) ging so weit, dass er die Funde von *Rhyniella cursor* als nicht zu den Collembolen gehörig aufs heftigste bestritt.

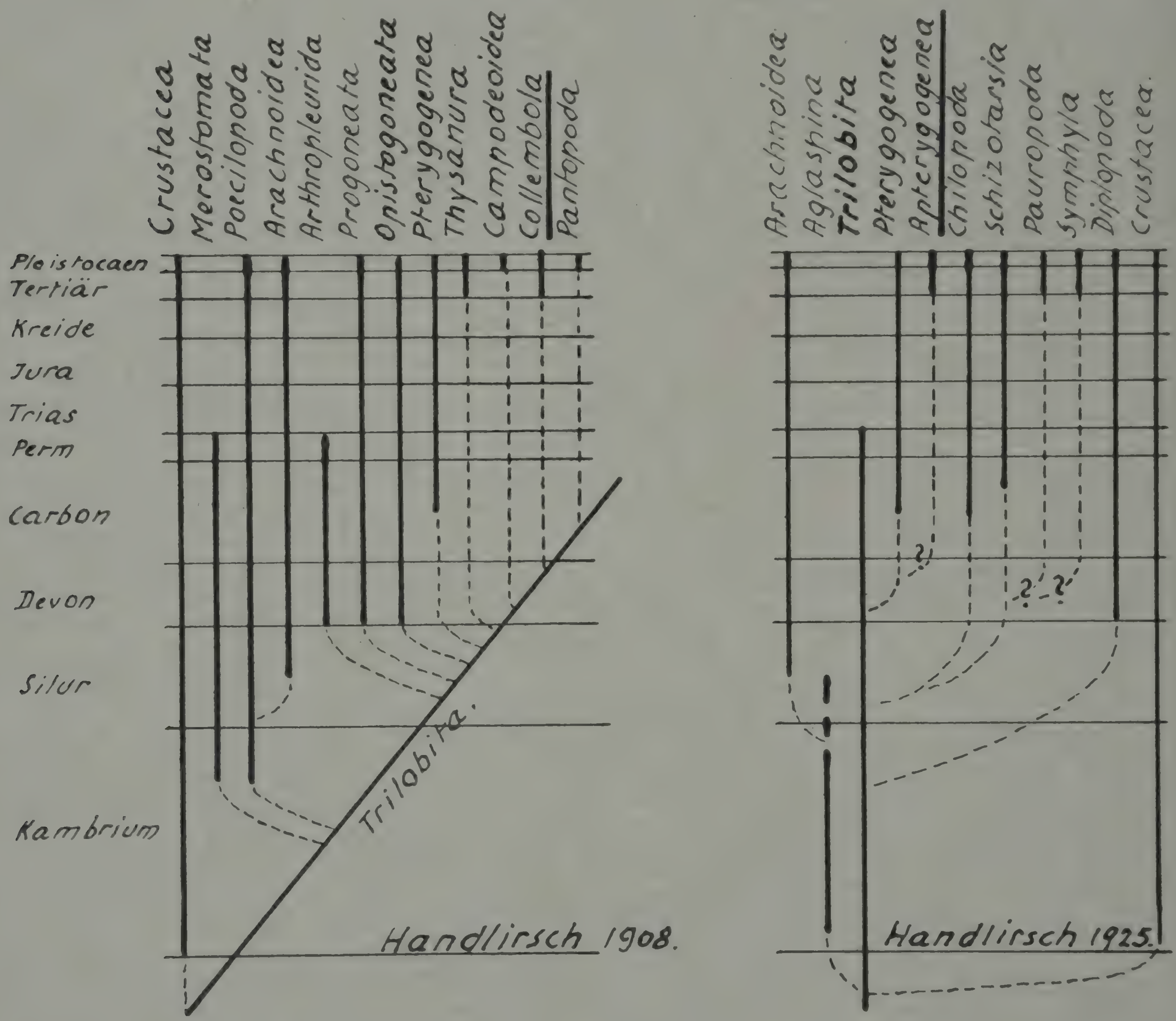

Crustacea
Merostomata
Poecilopoda
Arachnoidea
Arthropleurida
Progoneata
Opistogoneata
Pterygogenea
Thysanura
Campodeoidea
Collembola
Pantopoda
Pleistocaen
Tertiär
Kreide
Jura
Trias
Perm
Carbon
Devon
Silur
Kambrium
Trilobita.
Handlirsch 1908.
Arachnoidea
Aglaspina
Trilobita
Pterygogenea
Apterygogenea
Chilopoda
Schizotarsia
Pauropoda
Symphyla
Diplopoda
Crustacea
?
?
?
Handlirsch 1925.

Fig. 1.

Andererseits sieht Tillyard (1931) in den Charakteristica der Collembolen primitive Merkmale und baut darauf sein System auf, das von den Ptotomorpha, also den Collembolen ausgehend mehr oder weniger geradlinig zu den Pterygoten führt.

Die Collembolen sind für ihn älter als die Pterygoten, sie sind archaisch in ihrem Bau, also ancestral und nicht durch retrograde Entwicklung sekundär reduziert.

Beide betrachten aber die Collembolen nur im Hinblick auf die mögliche Ableitung der Pterygoten und nicht als Sonderfall einer speziellen Entwicklungsform, der zu einer gesonderten Stellung und Revision der Betrachtungsweise der Klasseneinteilung der "niedern" Arthropoden führen könnte.

An dieser Stelle setzen unsere Betrachtungen ein.

Wie dem auch sei, wir müssen festhalten, dass beide Untersuchungen wie auch alle ähnlichen der Periode vor und nach diesen beiden Entomologen, also auch die vorliegenden

Betrachtungen hypotetischer Natur sind und bleiben müssen. Sie sind Arbeitshypothesen, die umsomehr an Wahrscheinlichkeit gewinnen, je mehr Tatsachen zu ihrer Stütze zusammen getragen werden können. So soll auch hier nichts anderes als eine Diskussionsbasis geliefert werden, die veranlassen soll, das Problem der möglichen Ableitung auf eine neue Basis zu stellen, die zur Abklärung der Fragen notwendig erscheint.

Als Basis der Diskussion haben wir die speziellen Eigenschaften der Collembolen zu präzisieren und mit denjenigen anderer Gruppen der Arthropoden zu vergleichen. Dabei übergehe ich absichtlich diejenigen Punkte, welche morphologisch von untergeordneter Bedeutung nicht spezifisch sind oder die in der Arbeit von Remington (1953) schon eingehend umschreiben wurden.

Die Antennen sind primär 4-gliedrig. Durch sekundäre Aufteilung können 6 Glieder entstehen. Andererseits zeigt das 4. Antennenglied bei verschiedenen Formen die Tendenz einer sekundären Ringelbildung (*Tomocerus*, *Orchesella*, *Symphypleona*). Eine analoge Anlage finden wir bei den Jugendstadien der Diplopoden, nicht aber bei den Insekten und Thysanuren. Juvenilstadien der Diplopoden weisen 4 gliedrige Antennen auf.

Primär wird die Kopfkapsel aus 6 Segmenten gebildet, von denen die Anwesenheit eines Intercalarsegmentes oder des Praemandibulare wichtig ist. Es trägt im Embryonalzustand (Denis, 1928) noch Anhänge einer Praemandibel und ist aussen durch die Anwesenheit des Postantennalorganes gekennzeichnet. Wenn auch Imms (1951) erst die Anwesenheit der Praemandibel bezweifelte, so ist doch durch die Untersuchungen von Folsom (1900) und Denis ihre Anwesenheit genügend belegt. Dieses Praemandibularsegment spielt bei den Crustaceen eine grosse Rolle, als Träger der Antennulae. Es erscheint wieder bei den Proturen mit einem Postantennalorgan und ebenso bei den Symphylen und Diplopoden. Ob der Praeocellus der Pauropoden ein analoges Organ und dem gleichen Segmente zuzuweisen ist, muss noch festgestellt werden.

Eigenartig sind die entognathen Mundteile, doch dürfen wir sie trotzdem kaum zu Vergleichszwecken herbeiziehen. Sie sind nach der Beschaffenheit der Nahrung zu starken Aenderungen unterworfen. Die Mandibel, mit stark getrenntem Inzisiv-und Molarteil erinnert an diejenige der Machiliden, hat aber in keinem Falle eine Parallele bei den Insekten. Hingegen finden wir ihre Gestalt wiederum bei Sympoda unter den Krebsen vor. In der Maxille, welche auf einen kleinen Maxillenkopf zusammangedrängt ist, sind Analogien schwer zu deuten, doch lassen sich auch hier eher Vergleiche mit den Crustaceen und Chilopoden anstellen als mit höhern Formen.

Der stets flügellose Thorax besitzt 3 Segmente von denen das erste fast immer reduziert ist. Die 3 Beinpaare sind stets uniserial, tragen also keine Styli wie bei vielen Thysanuren und Symphylen. In ihrer Gliederung sind sie einfach. Auf die Tibia oder besser den Tibiotarsus folgt ein kleiner Praetarsus, der die einzige Klaue trägt. Ihr opponiert steht ein Empodium, oft mit Lamelle dem Empodialanhang ausgerüstet, der funktionell als Putzorgan dient, wie die Tibialborsten höherer Insekten.

Das Abdomen weist stets 6 Segmente auf. Diese Anzahl ist primär, embryonal festgelegt. Sie wird während der Entwicklung weder vergrössert noch reduziert. Dadurch stellen sich die Collembolen in Gegensatz zu allen andern Arthropodengruppen, bei welchen entweder Anamerie oder Epimerie vorkommt. Die Collembolen sind also holomer. Das 1., 4. und 5. Abdominalsegment tragen embryonal Beinknospen, die in den basalen Anlagen verschmelzen, distal aber i.d. Regel getrennt bleiben. Sie bilden später den Ventraltubus, das Retinaculum und die Furca, letztere mit beinartiger Gliederung.

Die Sexualöffnung befindet sich undifferenziert auf dem 5. Abdominalsegment, die Analöffnung liegt terminal.

In ontogentischer Hinsicht verhalten sich also die Collçmbolen was die abdominalen Anhänge anbetrifft gleich wie die Thysanuren s.l., wie die Symphylen und Chilopoden. Sie sind in dieser Hinsicht phylogentisch sicher älter als die Pterygoten, bei welchen embryonale Beine am Abdomen vorhanden sind, aber nicht zur Ausbildung kommen oder wie viele anamorphe Klassen, bei denen sie im Laufe der postembryonalen Entwicklung sukkzessive erscheinen.

Von den anatomischen Merkmalen seien nur die hervorstehendsten summarisch erwähnt. Das Fazettenauge fehlt. Im Maximum treten jegerseits 8 Ocellen auf, die einen Ommenfleck bilden. Mit Ausnahme von *Actaletes* unter den *Arthropleona* und den *Sym-*

phypleona besitzen die Collembolen kein Tracheensystem. Wo dasselbe zur Ausbildung kommt, bleibt es einfach. Aeussere Stigmen fehlen. Von der zwischen Kopf und Prothorax befindlichen Krypta dringen einfache Tracheenstämme in Kopf und Thorax ein. Malpighische Gefässe fehlen vollständig. Sie treten bei den Proturen als einfache Zellringe auf, finden sich aber in wechselnder Anzahl sowohl bei den Myriopoden s.l. den Thysanuren und Insecten. Das Germarium der Gonaden liegt lateral ähnlich wie bei vielen Pauropoden, den Symphylen, während es bei den Proturen, Thysanuren und Pterygoten apical gelagert ist.

Besonders wichtig für die phylogentische Beurteilung gestalten sich Fortpflanzung und Entwicklung der Collembolen.

Die Befruchtung erfolgt mittels Spermatophoren, die als kleine gestielte Kapseln vom Männchen der Unterlage angeheftet werden und die vom Weibchen aktiv mit den Valven abgenommen werden. Bei vielen Symphypleonen scheint die Befruchtung anders zu verlaufen. Die Männchen der Sminthuridesarten sind mit Greifantennen ausgerüstet. Levander (1894) hat Vorgänge geschildert, welche als Copulationsvorgang gedeutet worden sind. Sie müssen hingegen nach den neuen Befunden die wir Schaller (1952, 1953, a, b, 1954 a, b) verdanken, revidiert werden. In ähnlicher Weise findet die Befruchtung bei den Thysanuren, Scorpionen und Pseudoscorpionen statt. Auch dort werden die Spermatophoren vom ♀ aktiv aufgenommen, während bei Insekten, wo ebenfalls Spermatophoren bei denjenigen Gruppen ausgebildet werden, die lange Legestachel besitzen vom Männchen dem weiblichen Genitalporus angeheftet werden.

Die Embryonalentwicklung beginnt, wie die an den verschiedensten Formen aufgezeichnet worden ist [Claypole (1897, 1898a, b), Folsom (1900)—*Anurida;* Uzel (1897a, b, 1898)—*Tetradontophora*, *Tomocerus;* Uljanin (1875)—*Anurophorus;* Philiptschenko (1912) —*Isotoma*] entsprechend den dotterarmen Eiern mit einer totalen, äqualen Furchung, welche ungefähr auf dem 32 blastomeren Stadium durch Auswandern der Kerne, also einer Dotterzerklüftung, in eine superfizielle Furchung übergeht. Einzig die Sexualkerne bleiben in der Tiefe des Dotters liegen und bilden später die Gonaden aus. Dieser Modus der Entwicklung findet wohl eine Parallele bei gewissen parasitischen Hymenopteren mit ausgesprochener Polyembryonie. Sie sind deshalb sicher nicht miteinander vergleichbar. Bei den übrigen Arthropoden findet sich hingegen diese Art Eifurchung in weiter Verbreitung. Wir finden sie bei den Symphylen [*Hanseniella* (Tiegs 1945)], den Pauropoden (Tiegs, 1949) wo auch das charakteristische Dorsalogan zu finden ist, bei den Tyroglyphiden unter den Milben (Reuter, 1909) und bei gewissen Crustaceen (Entomostraken, Cirripedien und einzelnen Cladoceren). Die spezifische Eigenart der Eifurchung weist also in erster Linie zu den sogenannten primitivern Arthropoden hin. Die mit reichem Dotter ausgerüsteten Eier der Thysanuren s.l. und Insekten finden wir stets durch inaequale, superfizielle Furchung ausgezeichnet.

In gleicher Weise hat sich die postembryonale Entwicklung als für die Beurteilung der Zugehörigkeit zu den Insekten erwiesen. Bei Untersuchungen an *Orchesella*, die zum Zwecke unternommen wurden, die im Laufe der Zeit sich herausbildenden und sich verändernden Zeichnungsmuster festzuhalten, fand Lindenmann (1950), dass die Tiere mit ca. 15 Häutungen geschlechtsreif werden. Diese Zeit ist abhängig von der Temperatur, nicht von der Zeit. Sie schwankt zwischen 33 und 184 Tagen je nachdem die Eier im Sommer oder Spätherbst abgelegt worden sind.

Im ganzen machen die Tiere nun ca. 50 Häutungen durch, die sich oft über mehr als ein Jahr erstrecken können. Nach der ersten Eiablage folgen die Häutungen weiter und etwa nach einem Intervall von 5 Häutungen erfolgt ein weiterer Eischub. Dies wiederholt sich bis zum Tode des Tieres. Mit dem Erlangen der ersten Reife ist aber das Wachstum der Tiere nicht abgeschlossen. Bis zur 25. Häutung nimmt es noch ca. 70% an Länge zu. Von da an verlangsamt sich die Längenzunahme und bis zum Tode der Tiere wird nur noch ca. 10% an Länge zugesetzt. In dieser letzten Phase des Lebens, die bis zu einem Jahre dauern kann, verändert sich nun in erster Linie das Farbkleid, indem die Zeichnungsmuster sich ausdehnen und zusammenfliessen können. Männliche und weibliche Trachten beginnen sich zu differenzieren.

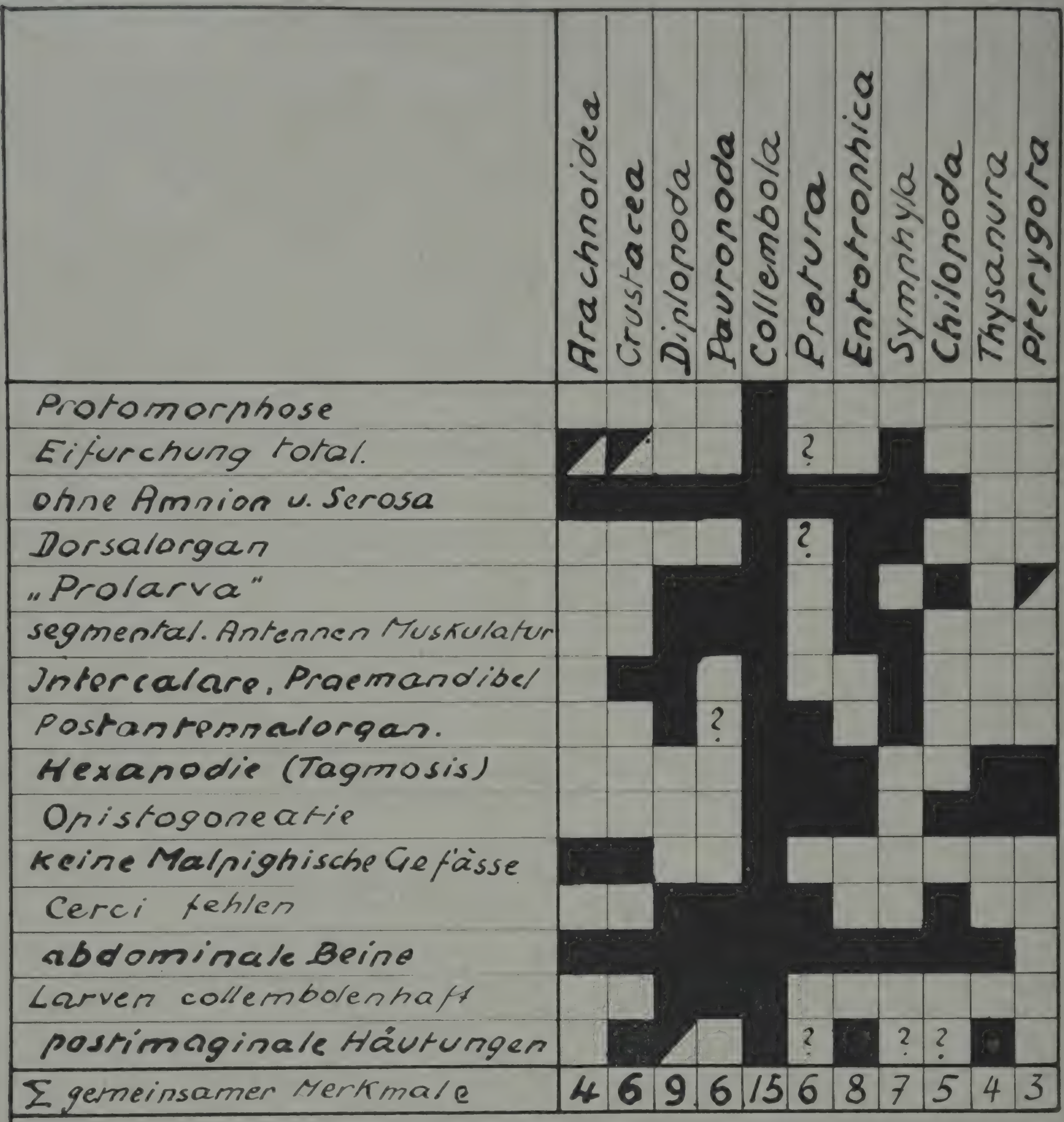
Wesentlich ist, dass die Erreichung der Reife und die erste Eiablage nicht den Tod des Tieres bedingt. Bei den Insekten, bei denen oft ebenfalls hohe Häutungszahlen festgehalten worden sind (Ephemeriden, Plecoptera) erreichen wie alle andern Insekten erst mit dem Eintritt in das imaginale Stadium, in die letzte Phase ihres Lebens, Maturität. Die Imago ist Fortpflanzungs- und Verbreitungsstadium. Bei den Collembolen wechseln Legeperioden und Ruhepausen in gewissem Rhytumus miteinander dauernd ab. Sie sind darum von den Insekten fundamental verschieden. Ganz analog im Verhalten ist nun *Astacus*, der nach der 15. Häutung im 2. Lebensjahre geschlechtsreif wird. Alle Jahre finden darauf hin 1—2 Häutungen statt, im ganzen ca. 50 während des ganzen Lebens und jedes Jahr tritt erneut Copulation und Eiablage ein. Gleichzeitig wie Lindenmann ist nun Sweetmann (1953) bei Untersuchungen an *Ctenolepisma* für die Lepismatiden zu analogen Ergebnissen gelangt, was mich in Zusammenhang mit dem ganzen Fragenkomplex veranlasste, durch meine Schüler von Orelli, Gyger und Schäfer die Campodeiden, Japygiden und Machiliden untersuchen zu lassen. Die teilweise vorliegenden abgeschlossenen Resultate dieser Untersuchungen zeigen folgendes Bild.

Alle Gruppen der Thysanura ectotrophica und endotrophica zeigen in Bezug auf die postembryonale Entwicklung das gleiche Bild wie die Collembolen. Die Zahl der Häutungen und damit in Verbindung der einzelnen Eischübe verschieben sich aber stark zu Gunsten eines einzigen Eischubes während der Dauer eines Jahres. Bei Campodea rhopalota, es wurden 5 Arten untersucht, zeigen sich bis zu 6 Eiablagen noch während eines Jahres. Bei Machiliden und Japygiden hingegen zeichnet sich eine einzige Ablage entweder im Frühling oder Sommer ab und die Intervalle zwischen den einzelnen Häutungen verlängern sich und werden unregelmässig. Man hat ganz allgemein dieser, sehr wichtigen Tatsache, bis jetzt viel zu wenig Beachtung geschenkt. Mit der Eiablage hat man in der Regel den Zyklus des Lebens als abgeschlossen betrachtet. Wenn auch Daiber aussagt, dass bei Chilopoden nach der Geschlechtreife eine Zunahme von Beinpaaren nachzweisen sei, so muss für die Chilopoden und Diplopoden doch eine Klärung dieser Frage neu erfolgen. Sie ist wichtig, da sich in diesem Verhalten besondere verwandtschaftliche Verhältnisse abzeichnen, denen man bis jetzt keine Beachtung geschenkt hat. Speziell sind in dieser Hinsicht auch die Chilopoda anamorpha und epimorpha, zu untersuchen, da das Vorkommen zweier verschiedener Entwicklungsformen in einer sonst scheinbar morphologisch änhlichen Gruppe von Tieren, die heute einer grossen Ordnung zugerechnet werden, revisionsberechtigt erscheint.

Als letztes, in erster Linie phylogentisch wichtiges Merkmal sei nochmals auf das geologische hohe Alter hingewiesen. Die Collembolen sind schon aus dem Devon bekannt. *Rhyniella cursor* (Hirst & Maulik, 1926) ist eine Collembole, die uns der Zufall in den Cordaitineenknollen der Rhyniabeds erhalten hat. Sie treten also gleichzeitig mit den ersten Diplopoden und Chilopoden auf, während die Insekten erst viel später im unteren Obercarbon in Erscheinung treten. Soviel die Reste zeigen, sind sie schon in voller und analoger Ausbildung vorhanden, wie die Formen des Tertiärs. Man kann sich nun einem Einzelfund gegenüber skeptisch verhalten. Doch muss er meines Erachtens Berücksichtigung finden, sogut wie alle andern Einzelfunde von Fossilien anderer Tiere, welche für die Beurteilung von stammesgeschichtlichen Fragen undiskutierbar dastehen.

Wenn wir nun die erwähnten Charaktere der Collembolen mit denjenigen der Anamorpha und Epimorpha vergleichen, ergibt sich ein Bild der gegenseitigen Beziehungen, das für sich selbst sprechen mag. (*cf.* Fig. 1). Wir halten die wichtigsten Merkmale der Collembolen als zentrale Gegebenheit fest und markieren die mit den andern Gruppen gemeinsamen Züge an entsprechender Stelle. Hier fällt uns auf, wie stark die gemeinsamen Merkmale sich gegen die Pauropoden, Symphylen und Myriopoden hin häufen, während Entotrophica, Thysanuren und gar Pterygoten mit den Crustaceen auf gleicher Stufe stehen, wobei es aber gerade bei den Crustaceen primitivere Merkmale sind, in denen sie sich gleichen, Merkmale, welche u.a. auch bei den Thysanuren s.l. auftreten, also den gesammten niedern Arthropoden eigen sind. Als gemeinsames Merkmal mit den Pterygoten bleibt eigentlich nur die Opistogoneatie und die Hexapodie der 3 ersten Leibessegmente übrig.

Von den durch Tillyard ins Feld geführten Argumenten muss uns in erster Linie die Holomerie interessieren, die einzig den Collembolen zukommt und die ihnen den eigenen Stempel aufprägt. Wir müssen erwägen, ob die definitive Fixierung der Segmente ohne weitere Möglichkeit auf eine Reduktion oder Vermehrung wirklich sei und ob sie uns genügen kann, die Stellung der Collembolen zu präzisieren. Beim hohen Alter der Collembolen scheint dies zunächst der Fall zu sein. Doch muss die Annahme leider hypothetisch bleiben, da wir keinerlei Anhaltspunkte besitzen, welche die Holomerie der alten Formen



	Arachnoidea	Crustacea	Diplopoda	Pauropoda	Collembola	Protura	Entotrophica	Symphyla	Chilopoda	Thysanura	Pterygota
Protomorphose					■						
Eifurchung total.	◤	◤			■	?		■			
ohne Amnion u. Serosa	■	■	■	■	■	■	■	■	■		
Dorsalorgan					■	?	■	■			
„Prolarva"			■	■	■		■		■		◤
segmental. Antennen Muskulatur			■	■	■		■	■			
Intercalare, Praemandibel		■	■		■			■			
Postantennalorgan.			■	?	■	■		■			
Hexapodie (Tagmosis)					■	■	■			■	■
Opistogoneatie					■	■	■		■	■	■
keine Malpighische Gefässe	■	■			■						
Cerci fehlen			■	■	■	■			■		
abdominale Beine	■	■	■	■	■	■	■	■	■	■	
Larven collembolenhaft			■	■	■						
postimaginale Häutungen		■	◤		■	?	■	?	?	■	
Σ gemeinsamer Merkmale	4	6	9	6	15	6	8	7	5	4	3

Fig. 2.

beweist. Sicher setzt die Fixierung auf 9 Segmente im Gegensatz zu den übrigen Formen, sowohl zu den Myriopoden als zu den Epimera eine Eigenart voraus. Nur bei den Pauropoden werden 6—10 Segmente (tergal) mit 9 Beinpaaren denen 6 bei den Collembolen gegenüber stehen, angelegt. Diplopoden und Pauropoden besitzen nun Larvenformen mit 3 Beinpaaren und 2—4 Abdominalsegmenten von typisch collembolenhaftem Aussehen. Wenn wir nun auch der Aehnlichkeit von Larvenformen mit den Adultstadien keine zu hohe Bedeutung zumessen dürfen, so finden wir doch immer Bezugnahme auf solche Fälle in phylogenetischer Hinsicht, die besonders an Wert gewinnen, wenn noch andere morphologische Merkmale in Uebereinstimmung vorhanden sind. So treten denn die Collembolen in ihrer definitiven Gestaltung den Diplopoden und Pauropoden näher als den Symphylen, welche in ihrer Form eher auf die Entotrophica und Thysanuren hinweisen, während die Jugendgestaltung der Diplopoden und die Adultform der Collembolen zueinander direkte Beziehungen zu haben scheinen. Wenn nun auch die Anamerie-Epimerie als teilweise in den Gruppen sich ablösende Eigenart der Arthropoden im weitesten Sinne in Erscheinung tritt, ich denke dabei besonders an die Chilopoda anamera und epimera, und die Protura, so bin ich doch mit Tillyard der Ansicht in der Protomorphose ein besonders altertümliches Merkmal zu sehen und in der Form der Collembolen eine altertümliche Gruppe, aus welcher sich sowohl Pauropoden und Chilopoden entwickelt haben können. Zu dieser Annahme darf auch das hohe geologische Alter gerechnet werden, denn die

Collembolen treten mit den Diplopoden und Chilopoden etwa gemeinsam auf. Die Collembolen können deshalb als eine frühzeitig zur Ruhe gekommene Entwicklungsform angesehen werden, aus welchen sich sowohl anamorphe wie auch epimorphe Stämme entwickelt haben können. Andererseits kennen wir aber bei den Crustaceen keine protomorphen Stämme, sowenig wie bei den andern Arthropoden was auch auf eine sekundäre Entwicklungsform hinweisen würde. Wie dem auch sei, dürfen wir die Collembolen auf keinen Fall mit den höhern Insekten in Verbindung bringen, wie dies bis jetzt in der alten Gruppe der Apterygogenea geschehen ist.

In dieser Hinsicht stellt uns auch die Fixierung des Gonoporus vor das gleiche Problem. Bei den Collembolen liegt er stets auf dem 8. postcephalen Segmente, für Männchen und Weibchen undifferenziert. Er ist in dieser Hinsicht eindeutig opistogoneat. Bei den Chilopoden findet sich das 7.—9. Segment für seine Aufnahme praedestiniert, während er bei den Pauropoden und Symphylen weiter nach vorne wandert. Die Thysanuren im alten Sinne und die Pterygoten bilden den Gonoporus auf dem 14. resp. 15. Segmente aus während bei den noch eine rudimentäre Anamerie besitzenden Proturen er auf dem 14. Segmente liegt.

Generell werden durch die Entwicklung Pauropoden, Symphylen und Collembolen nahe zusammengeführt. Sie sind identisch in Bezug auf die ersten Furchungsvorgänge, wie auch in der Ausbildung des Dorsalorgans. Parallelen finden sich in dieser Hinsicht bei den Crustaceen und Milben. Generell unterscheiden sie sich aber von den Diplopoden und Chilopoden und Thysanuren, bei welchen an Stelle der anfänglich totalen aequalen Furchung eine von centralem Kerne ausgehende Bildung von Dotterpyramiden eintritt, die nach der Dotterzerklüftung in eine superfizielle Furchung übergeht. Nicht untersucht sind in dieser Hinsicht die Proturen, sodass deren definitive Eingliederung noch nicht möglich ist.

Als vollständig verschieden von den Insekten haben sich auch das postembryonale Verhalten und die über die erste Reife hinausgehenden Häutungen erwiesen, welche sie mit den Entotrophica und Ectotrophica teilen. Sie gleichen in dieser Hinsicht den Crustaceen. Auch hier fehlen ergänzende Untersuchungen für die Myriopoden auf der ganzen Linie. Fassen wir die vorliegenden Resultate zusammen:

In den beiden letzten grossen Deutungsversuchen über die Ableitung der Pterygota, denen auch die neuen Hand- und Lehrbücher von Kückenthal, Grassé, Imms etc. folgen, wenn auch teilweise mit angedeuteter Reserve, werden die Apterygogenea und Pterygogenea als Stämme der Hexapoda behandelt. In den Diskussionen werden sie als Einheiten einander gegenübergestellt.

Die Apterygoten sind nun aber sicher keine Einheit. Ihre Charakteristica sind divers und zeigen Anklänge zu den verschiedensten Gruppen. Diese Eigenarten verlangen bei einer Zuteilung dringend Beachtung.

Während Handlirsch der Entwicklungsform untergeordneten Charakter beimisst, steht dieselbe für Tillyard im Vordergrunde. In seinen Uebergruppen gliedert er, sich folgend, jeweilen Protomorpha, Anamorpha und Epimorpha ab, Stufen die für ihn phylogenetischen Wert besitzen, wie er auch den hypotethischen Protaptera protomorphen Charakter zuweist. So leitet er in gerader Linie von den Collembolen, aus denen sich auch die Myriopoden entwickeln, die Proturen, Entotrophica, Ectotrophica und Pterygoten ab. Nachdem ich schon 1951 und erneut 1955 auf die Isoliertheit der Collembolen in systematischer Hinsicht hingewiesen habe, erhielt ich bei der Ausarbeitung der vorliegenden Studie, die Arbeiten Remington "The Apterygota" in welcher zur systematischen Einordnung der Collembolen Stellung genommen wird. Die Collembolen stehen nach ihm im Subphylum der Insecta, welches neben den eigentlichen Pterygoten die gesammten Myriopoden umfasst. Nach dem Fehlen oder Vorhandensein von Amnion und Serrosa, eines Ovipositors und Phallus und der innern (intrinsic) Antennmuskulatur werden 2 Sektionen, die Myocerata und Amyocerata unterschieden. Die Collembolen werden nun mit den Proturen, Symphylen und Entotrophen zu den Labiata zusammengefasst, welchen als Ueberklassen die Chilopoden Trignatha einerseits und die Pauropoden mit den Diplopoden Dignatha gegenüberstehen.

In der Klasse der Labiata haben wir nun neben den erwähnten allgemeinen Zügen Formen vor uns, welche sowohl protomorph, anamorph und epimorph sind. Eine Trennung dieser heterogenen Gruppe scheint mir deshalb den Tatsachen besser zu entsprechen, da sie in der jetzigen Form immer noch den verwirrenden Status der alten Apterygogenea in gewisser Hinsicht aufrecht zu erhalten sucht. Bezüglich der Einordnung zu den 3 Klassen der Myocerata in Dignatha, Trignatha und Labiata, möchte ich hervorheben, was früher schon festgehalten wurde. Trotz Aehnlichkeiten muss gerade dem Bau der Mundteile nicht zu grossen Wert beigemessen werden, da sie von Fall zu Fall nach der Nahrung zu starken Aenderungen unterworfen sind.

So bin ich der Ansicht, dass den einzelnen Ordnungen der *Labiata* besser Klassenwert zuerteilt wird. Die Gruppierung derselben zu denjenigen Formen, mit welchen sie wirkliche Beziehungen haben, wird dadurch nicht nur erleichtert, sondern sicher sinnvoller.

In diesen Ausführungen war es notwendig, da es mir um die Fixierung der Stellung der Collembolen ging, die niedern Gruppen der Arthropoden etwas näher zu betrachten.

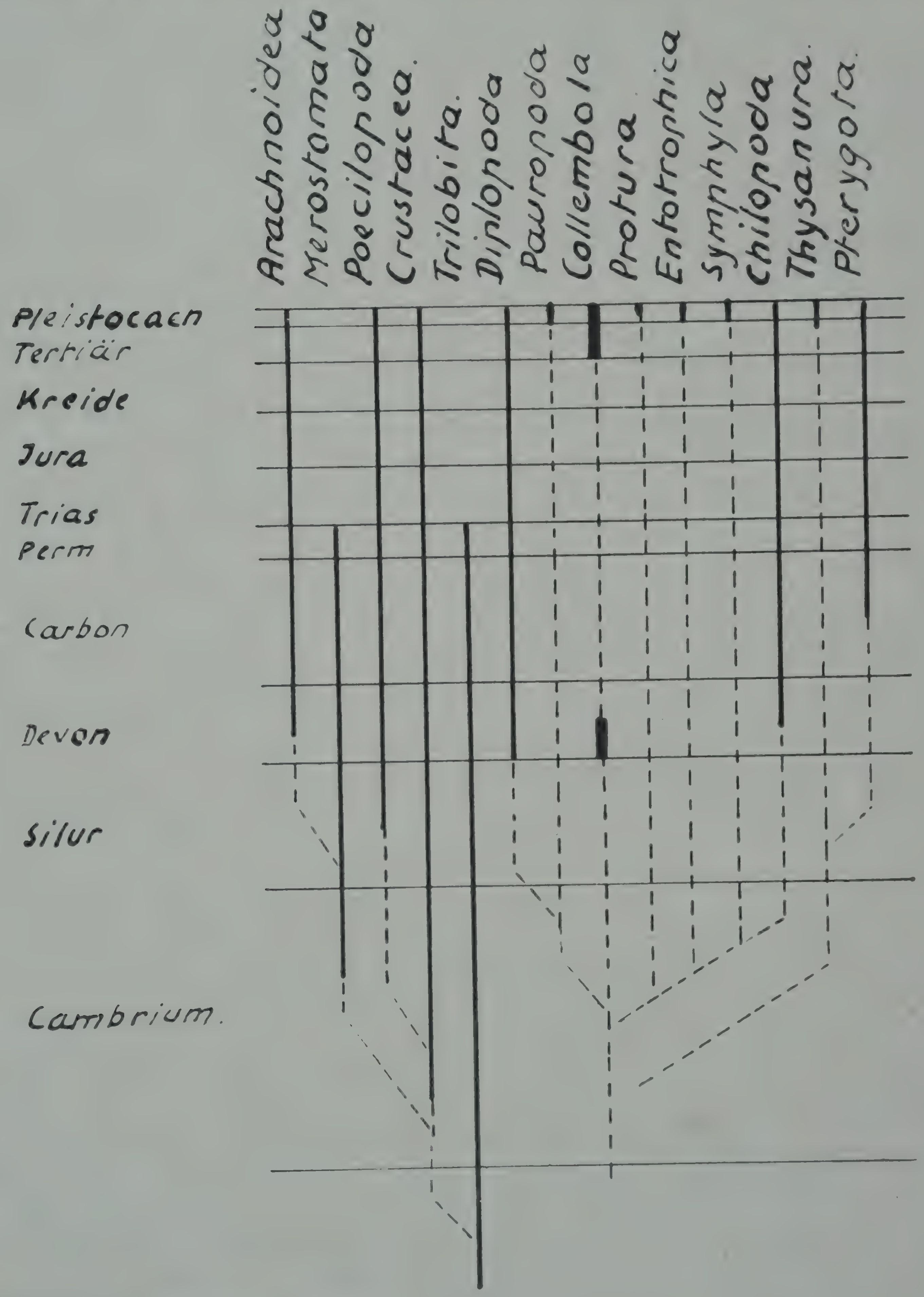

Arachnoidea
Merostomata
Poecilopoda
Crustacea.
Trilobita.
Diplopoda
Pauropoda
Collembola
Protura
Entotrophica
Symphyla
Chilopoda
Thysanura.
Pterygota.
Pleistocaen
Tertiär
Kreide
Jura
Trias
Perm
Carbon
Devon
Silur
Cambrium.

Fig. 3. Ableitung der Arthropoden (Handlirsch).

Wenn wir vom neuen System Remington's ausgehen und die bereits bestehenden Tatsachen, dass eigentlich die Chilopoden von den Diplopoden entfernt stehen und eher sich an die Insecta anreihen lassen, so kommen wir zur Konzeption, welche ich 1955 in den "Consideration sur la position systématique des Collemboles" festgehalten habe. Seine Labiata, welche dignath sind wie die Dignatha aber entothrophe Mundteile haben (mit

Ausnahme der Symphylen) haben bloss umgestellt zu werden, dass die Reihenfolge Dignatha-Labiata-Trignata entsteht, um eine natürliche Folge zu erhalten. Wir erhalten dann auch eine Reihe von Klassen, in welchen die Anlage der abdominalen Beine, erst von den Styli und Abdominalsäckchen ausgehend sich bis zur vollen Ausbildung dieser Organe steigert und die dann in der Klasse der Chilopoden zur vollen Ausbildung, unter Verlust der Stylusbildung kommt. Parallel entwickeln sich aber aus der gleichen Quelle kommend die Insecta mit Ovipositor und Phallusbildung mit den beiden Gruppen der Thysanuren und Pterygota. Wir kommen unter möglichster Beibehaltung der bestehenden Nomenklatur demnach zu folgendem Bilde:

Phylum: Arthropoda
Subphylum: Tracheata (Insecta Rem.)

Section: Myocerata (Rem.)
Klasse: Protomorpha
Ordnung: Collembola
Klasse: Myriopoda (Dignatha Rem.)
Ordnung: Pauropoda
Ordnung: Diplopoda
Klasse: Anamerentoma
Ordnung: Protura
Klasse: Entotrophica
Ordnung: Campodeida
Ordnung: Japygida
Klasse: Symphyla
Klasse: Chilopoda
Ordnung: Anamorpha
Ordnung: Epimorpha

Section: Insecta (Amyocerata Rem.)
Klasse: Thysanura
Ordnung: Lepislmatidae
Ordnung: Machilidae
Klasse: Pterygota

Die Umbenennung der ganzen Gruppe in Insecta scheint mir unnötig und nur verwirrend, es sollte dieser Begriff auf die Pterygoten und ihre nächsten Verwandten beschränkt bleiben, wie im allgemeinen auch hier die Nomenklaturregeln soweit als möglich zur Anwendung kommen sollten.

LITERATURVERZEICHNIS

Claypole, A. M. 1897. Some points on cleavage in Apterygota. *Trans. amer. micr. Soc.* 19: 74–82.
Claypole, A. M. 1898a. The embryology and oögenesis of *Anurida maritima* (Guér.). *J. Morphol.* 14: 219–300.
Claypole, A. M. 1898b. The embryology of the Apterygota. *Zool. Bull.* 2: 69–76.
Denis, J. R. 1928. Etude sur l'anatomie de la tête de quelques Collemboles, suivies de considérations sur la morphologie de la tête des insectes. *Arch. Zool. exp. gén.* 68: 1–291.
Denis, J. R. 1949. Sous-classe des Aptérygotes. *In*: P.–P. Grassé, Traité de Zoologie 9: 111–275.
Folsom, J. W. 1900. The development of the mouth-parts of *Anurida maritima* Guér. *Bull. comp. Zool. Harvard Coll.* 36: 87–157.
Handlirsch, A. 1908. Die fossilen Insekten und die Phylogenie der recenten Formen. Leipzig.
Handlirsch, A. 1925. Palaeontologie (Apterygota). *In*: C. Schröder, Handbuch der Entomologie 3: (215–216) Jena.
Handlirsch, A. 1930. Erste Unterklasse der Insekten, Apterygogenea oder Apterygota. *In*: Kükenthal & Krumbach, Handbuch der Zoologie 4 (1): 590–618. Berlin & Leipzig.
Handlirsch, A. 1937. Neue Untersuchungen über die fossilen Insekten, mit Ergänzungen und Nachträgen (etc.). *Ann. naturh. Mus. Wien* 48: 1–140.
Handschin, E. 1926. Collembola—Springschwänze. *In*: Schulze, Biologie der Tiere Deutschlands 25 (20): 7–56.
Handschin, E. 1953. Die Bedeutung der postembryonalen Entwicklung für die Protomorpha (Collembolen). *Congr. int. Entomol. 9. Trans.* 1: 235–240. (=1951, Amsterdam).
Handschin, E. 1955. Considérations sur la position systemetique des Collemboles. *Mém. Soc. R. d'Ent. Belgique.* 27: 40–53.
Handschin, E., & W. Lindenmann. 1948. Beobachtungen über die postembryonale Entwicklung von *Orchesella*. *Verh. schweiz. naturf. Ges. (Aarau)* 128: 154–156.
Hirst, S., & S. Maulik. 1926. On some arthropod remains from the Rhynie Chert (Old Red Sandstone). *Geol. Mag.* 63: 69–70.

Imms, A. D. 1939. On the antennal musculature in insects and other arthropods. *Quart. J. micr. Sci.* 81: 273–320.

Imms, A. D. 1951. A general textbook of entomology. Ed. 1 = 1930, ed. 3 = 1934, ed. 4 = 1938, ed. 5 = 1942, ed. 6 = 1947, ed. 8 = 1951. London.

Imms, A. D. 1947. The phylogeny of insects. *Tidj. Ent.* 88: 63–66.

Lang, A. 1889. Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere. Jena.

Levander, K. M. 1894. Einige biologische Beobachtungen über *Sminthurus apicalis* Reuter. *Acta Soc. Fauna Flora Fenn.* 9(9): 1–10.

Lindenmann, W. 1950. Untersuchungen zur postembryonalen Entwicklung schweizerischer Orchellen. *Rev. Suisse Zool.* 57: 353–428.

Philiptschenko, J. 1912. Beiträge zur Erkenntnis der Apterygoten. III. Embryonalentwicklung von *Isotoma cinerea* Nic. *Z. wiss. Zool.* 103: 519–660.

Remington, C. L. 1953. The "Apterygota". *In*: A Century of Progress in the Natural Sciences. 1853–1953. (pp. 495–505).

Reuter, E. R. 1909. Zur Morphologie und Ontogenie der Acariden. Mit besonderer Berücksichtigung von *Pediculopsis granicum* (Reut). *Acta Soc. Scient. fenn.* 36.

Schaller, F. 1952. Die "Copula" der Collembolen (Springschwänze). *Naturwissenschaften* 39: 48.

Schaller, F. 1953a. Das Fortpflanzungsverhalten apterygoter Insekten (Collembolen und Machiliden). *Verh. dtsch. zool. Ges.* (1952): 184–189.

Schaller, F. 1953b. Untersuchungen zur Fortpflanzungsbiologie arthropleoner Collembolen. *Z. Morphol. Oekol. Tiere* 41: 265–277.

Schaller, F. 1954a. Indirekte Spermatophorenübertragung bei Campodea (Apterygota, Diplura). *Naturwissenschaften* 41: 406–407.

Schaller, F. 1954b. Die indirekte Spermatophoren-Uebertragung und ihre Probleme. *Forsch. Fortschr.* 28: 321–326.

Sweetman, H. 1953. The number of instars among the Thysanura as influenced by environment. *Congr. int. Entomol.* 9. *Trans* 1: 411–415. (=1951, Amsterdam).

Sweetman, H. & F. W. Whittemore. 1937. The number of molts of the fire brat (Lepismatidae, Thysanura). *Bull. Brooklyn entomol. Soc.* 32: 117–120.

Tiegs, O. W. 1942. The "dorsal organ" of collembolan embryos. *Quart. J. micr. Sci.* 83: 153–170.

Tiegs, O. W. 1943. The "dorsal organ" of the embryo of *Campodea*. *Quart. J. micr. Sci.* 84: 35–48.

Tiegs, O. W. 1945. The post-embryonic development of *Hanseniella agilis* (Symphyla). *Quart. J. micr. Sci.* 85: 191–328.

Tiegs, O. W. 1949. The development and affinities of the Pauropoda, based on a study of *Pauropus silvaticus*. *Quart. J. micr. Sci.* 88: 165–336.

Tillyard, R. J. 1931. The evolution of the class Insecta. *Pap. Proc. r. Soc. Tasmania* (1930): 1–89.

Uljanin, V. N. 1875. Nabljudenija nad razvitijem Podur. *Izvest. imp. Obsc. Jestestvozn.* 16(3): 1–12.

Uzel, H. 1897a. Vorläufige Mittheilung über die Entwicklung der Thysanuren. *Zool. Anz.* 20: 125–132.

Uzel, H. 1897b. Beiträge zur Entwicklungsgeschichte von *Campodea staphylinus*. *Zool. Anz.* 20: 232–237.

Uzel, H. 1898. Studien über die Entwicklung der apterygoten Insecten. Königgrätz.

Willem, V. 1900. Recherches sur les Collemboles et les Thysanoures. *Mem. Acad. r. Sci. Belg.* 58: 1–144.

DISCUSSION

M. S. Ghilarov. In seinem wertvollen Vortrag hat Dr. Handschin aufs Neue die Angaben gegen A. Handlirschs Auffassungen gebracht und eine neue Handvoll Erde auf das Grab dieser Auffassungen geworfen wie es schon auch andere Forscher, und unter ihnen auch ich, nicht um einmal gemacht haben.

Die Angaben von Dr. Handschin uber die Besonderheiten von Collembolen sind, meiner Meinung nach, sehr überzeugend und ich glaube, dass die Zeit gekommen ist, die Collembolen, sowie auch Proturen und Dipluren, als selbstständige Klassen aus der Klasse der Insekten auszuschliessen.

Diese Meinung habe ich schon in meiner Monographie (1949) formuliert und Angaben zu ihren Gunsten sind auch in den späteren Arbeiten meines jüngeren Kollegen A. Sharov zu finden.

C. Delamare. Les particularités des gonades des Collemboles et l'ensemble de leur comportement méritent d'être soulignés. La possession par les Collemboles d'un grand nombre de caractères qui se trouvent disjoints par les autres groupes d'Arthropodes est un indice d'ancienneté. Tout ceci c'est le fond commun qui s'est différencié ailleurs. Le *Rhyniella* est un Pseudachoritini. Les faucilles actuelles devaient être différenciées au Dévonien.

Die systematische Stellung der Apterygota

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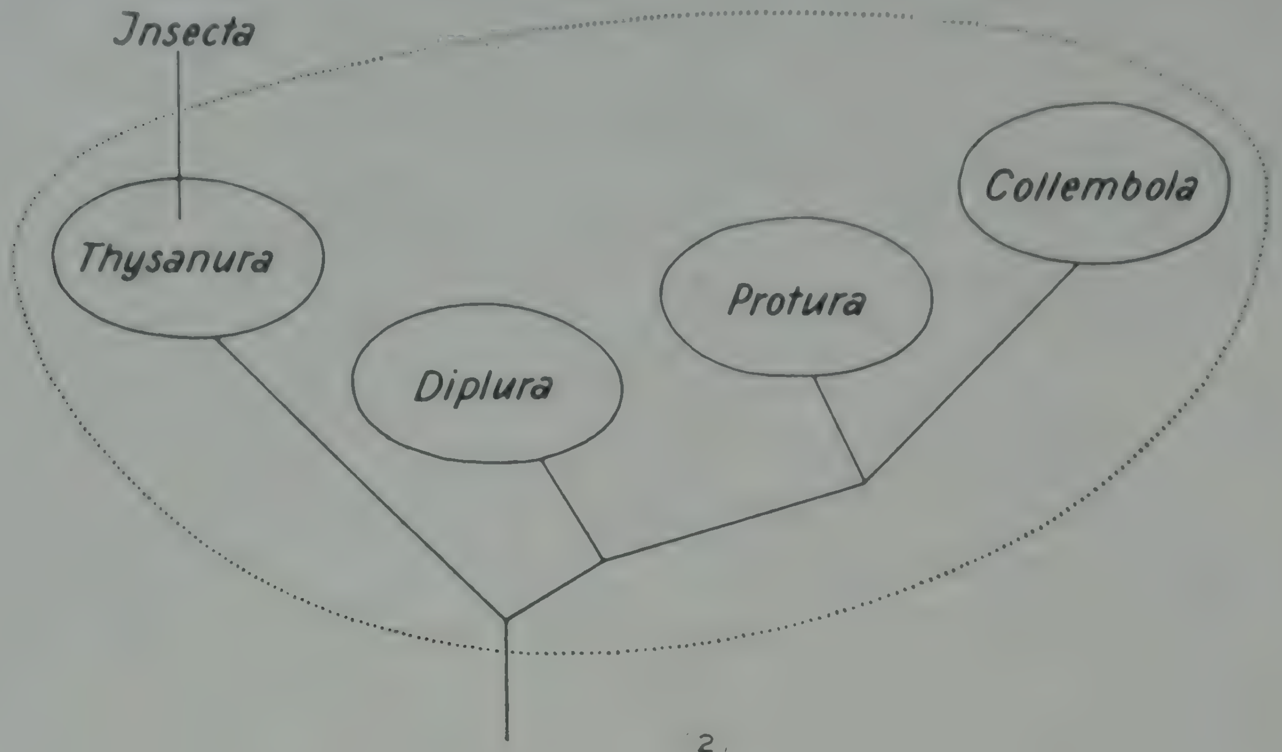
ABSTRACT

The author accepts the view of some specialists on the various groups of Apterygota, i.e. that those animals show many characteristics of their own, and cannot be included in the Insecta. However, he is opposed to the opinion, based on aberrant specialization of certain groups, that the individual sections of Apterygota were developed independently, and that they are not directly related. It is maintained that within the Antennata the reduction in the number of legs to 3 pairs has occurred only once. For this reason the relationship between the Insecta (Pterygota) and the various groups of Apterygota is considered to be a natural one. However, the Apterygota are more primitive in many respects than are the Insecta. The Apterygota agree in a considerable number of characters with the Symphyla, from which they differ principally in the development of only 3 pairs of functional legs, a feature which they share with the Insecta. Besides the Symphyla have the genital openings between the third and fourth pair of legs. The fact that in the Apterygota they are shifted caudad is obviously due to the beginning reinforcement of the thorax which causes the viscera to be moved posteriad into the abdomen; these conditions were transmitted to the Insecta. This development is not homologous to the conditions found in the Chilopoda, where the position of the genital openings is on the penultimate segment. In the Pauropoda and Diplopoda, which also are derived from the Symphyla, the genital openings are shifted cephalad, posterior to the second pair of legs. The Apterygota are considered to be a separate class which is placed between the classes Symphyla and Insecta. The relationships between the different classes of Antennata are shown in Fig. 1. Fig. 2 shows the connections within the Apterygota. The line leading to the Thysanura is ancestral to the Insecta (Fig. 3). The other line attains the highest degree of specialization in the Collembola. These are to be considered as a strongly specialized branch of an essentially primitive group. The Apterygota have developed locomotion by walking on 3 pairs of legs. In the Insecta development of movable articulated lateral processes of the dorsal plane of the reinforced thorax has resulted in locomotion by flying.

Zunächst schien es keine Schwierigkeiten zu bereiten, die mit 3 thoracalen Beinpaaren ausgerüsteten und ursprünglich flügellosen Antennaten in die Klasse der Insecta einzureihen. Gewissen Besonderheiten trug man bekanntlich dadurch Rechnung, dass man diese Tiere als Apterygota den als Pterygota zusammengefassten übrigen Insekten gegenüberstellte, welche beiden Einheiten man meist als Unterklassen ansprach. Die neuzeitliche Untersuchung der einzelnen Apterygoten-Gruppen ergab jedoch nicht allein zahlreiche morphologische und anatomische Abweichungen dieser Tiere von den Pterygoten, sondern auch auffällige Sonderausbildungen innerhalb der einzelnen Einheiten. Manche Spezialisten kamen daher zu dem Ergebnis, dass die systematische Vereinigung der Apterygoten mit den Pterygoten zu lockern wäre, ausserdem aber, dass die einzelnen Apterygoten-Gruppen unabhängig voneinander entstanden sind und miteinander keine näheren Verwandtschaftsbeziehungen haben. So hat beispielsweise Handschin (1952, p. 238) die Collembolen als besondere Klasse ausserhalb der übrigen Hexapoden aufgefasst, der er einen Platz an der Basis der Arthropoden zuweisen will und zwar noch vor der Abzweigung der Chelicerata.

Meines Erachtens hat man oft gewisse Sonderanpassungen einzelner Gruppen systematisch zu hoch bewertet und darüber die offensichtlichen Zusammenhänge missachtet. Ich bin der Ansicht, dass die so charakteristische Reduktion auf 3 postcephale Beinpaare innerhalb der Antennata nicht mehrmals erfolgt sein kann, dass also alle Formen miteinander verwandt und einheitlichen Ursprungs sind, die 3 thoracale Beinpaare besitzen. Somit ist anzunehmen, dass alle hexapoden Antennaten derselben Wurzel entsprossen sein müssen. Vergleicht man nun die Pterygoten mit den Apterygoten, so dürfte nicht zu übersehen sein, dass die erstere Gruppe die höher spezialisierten Formen umfasst und dass die Apterygoten, trotz zahlreicher Sonderbildungen einzelner Gruppen, weit primitivere Merkmale aufweisen, vor allem aber noch postadulte Häutungen durchführen, wie sie beispielsweise von Crustaceen seit langem bekannt sind, bei Pterygoten jedoch niemals vorkommen.



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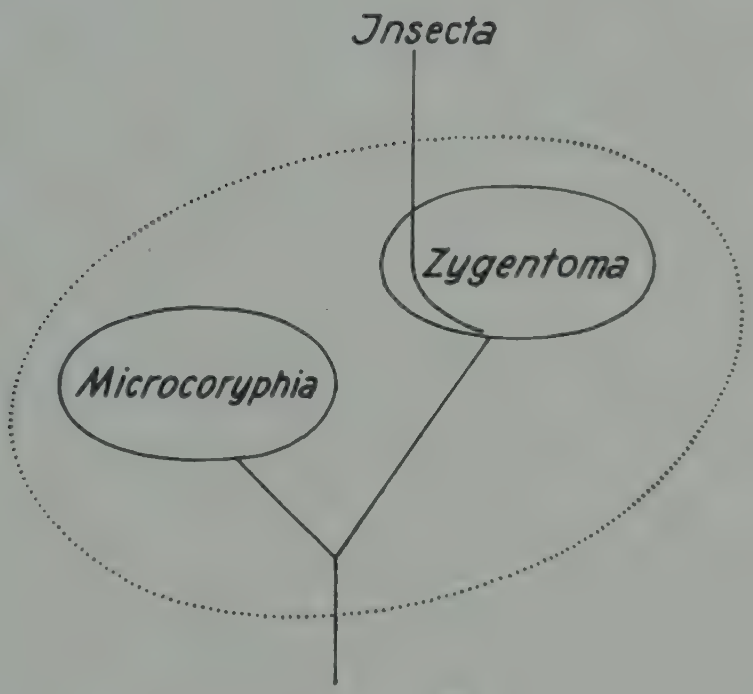

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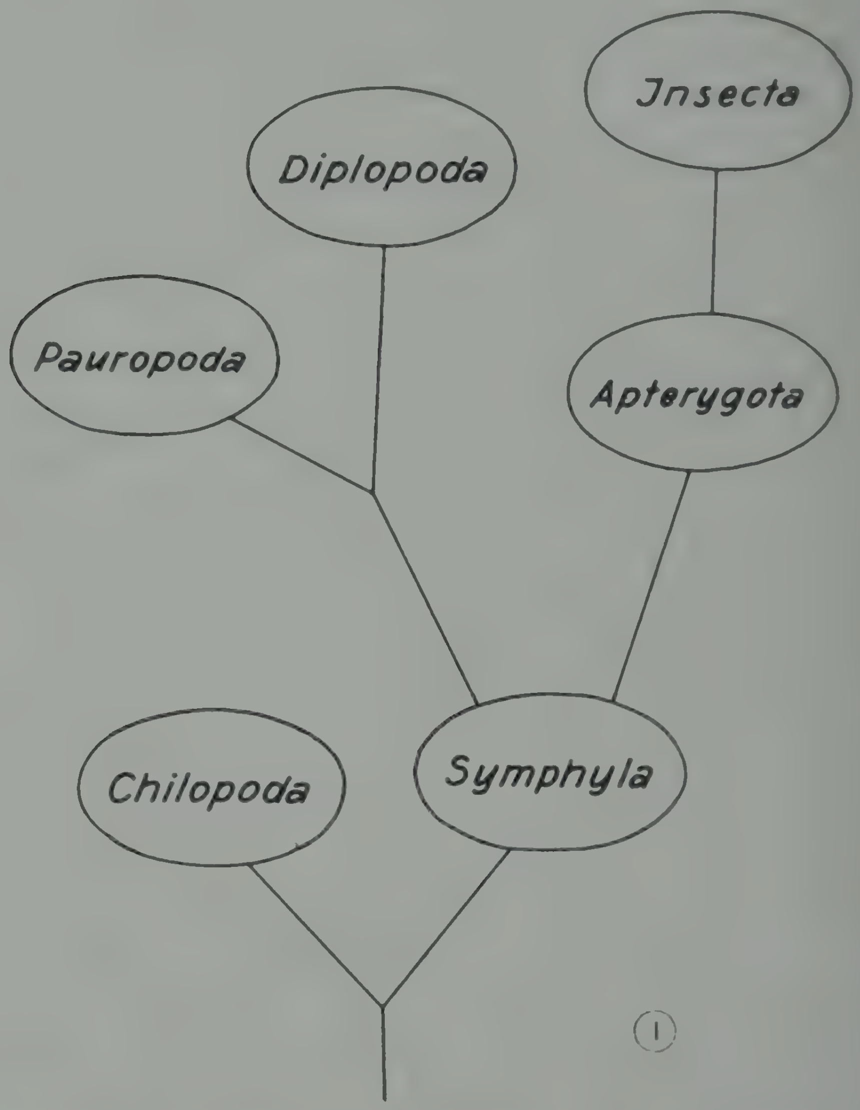

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Abb. 1. Verwandtschaftsbeziehungen der einzelnen Klassen der Antennata untereinander. Abb. 2. Verwandtschaftsbeziehungen der einzelnen Ordnungen der Apterygota untereinander. Abb. 3. Verwandtschaftsbeziehungen der beiden Unterordnungen der Thysanura und der von ihnen abzuleitenden Insecta.

Sucht man unter den übrigen Antennaten Verwandtschaftsbeziehungen mit den Apterygoten, so sind solche mit den Symphyla unverkennbar. Die Apterygoten sind eigentlich nichts anderes als auf 3 Beinpaaren laufende Symphylen, und viele morphologische Besonderheiten bei den Apterygoten sind nur eine Folge dieser veränderten Fortbewegungsart. Dass die Apterygoten von Antennaten mit einem Beinpaar an jedem Segment abzuleiten sind, ist schon daraus ersichtlich, dass bei ihnen ausser den 3 Paar thoracaler Beinpaare in verschiedenem Ausmass noch reduzierte oder veränderte abdominale Gliedmassen vorhanden sind. Bekanntlich bringt es die neue Fortbewegungsart mit sich, dass sich am Körper nunmehr 3 Segmentkomplexe in zunehmendem Ausmass gegeneinander abgrenzen: Kopf, Thorax und Abdomen. Es spezialisiert sich also der Lokomotionsapparat immer mehr auf den aus 3 Segmenten bestehenden Thorax, wodurch der grösste Teil des Verdauungstractus und der Geschlechtsapparat hauptsächlich in das Abdomen verschoben wird. Daher erscheint auch die unterschiedliche Lage der Geschlechtsöffnungen bei den Symphyla und den Apterygota verständlich. Es hätte sich dann die bei den Symphylen zwischen dem 3. und 4.

Beinpaar befindliche Geschlechtsöffnung bei den hexapoden Apterygoten nach hinten zum Ende des Abdomens hin verlagert; die rückwärtige Lage der Geschlechtsöffnung ist von den Apterygoten auch an die Insekten (Pterygoten) vererbt worden. Stets aber befinden sich die Geschlechtsöffnungen bei den einzelnen Gruppen jeweils auf einem ganz bestimmten Segment. Aus diesem Grund ist es nicht etwa möglich, wegen der Lage der Genitalöffnungen im hinteren Abschnitt des Körpers Apterygoten und Insekten mit den Chilopoden systematisch in Verbindung zu bringen, wie das Verhoeff (1910, p. 9) getan hat, als er Chilopoden und Insekten als Opisthogoneata den übrigen als Progoneata zusammengefassten Antennaten gegenüberstellte. Bei den Chilopoden liegt zwar die Genitalöffnung am vorletzten Segment; doch ist sie nicht etwa auf ein bestimmtes Segment fixiert, weil die Zahl der vorhergehenden Segmente variabel ist. Bereits Snodgrass (1938, pp. 144–145) hat auf diesen Umstand hingewiesen.

Anscheinend sind die Verhältnisse in der Lage der Genitalöffnung am vorletzten Segment, wie sie sich bei den Chilopoden finden, für die Antennaten als ursprünglich anzusehen. Auch sonst weisen die von mir als Klasse aufgefassten Chilopoda manche primitive Merkmale auf, vor allem die Arten der Unterklasse Notostigmophora, von denen die zweite, die Pleurostigmophora, abzuleiten sind. Zu erwähnen ist vor allem das Vorhandensein einer Ventralarterie, in die das Blut aus dem Herzen durch 1—3 Paar Seitenschlingen gelangt. Wenn auch bei manchen anderen Antennaten ein gut entwickeltes Arteriensystem vorhanden sein kann, so ist doch sonst nirgends noch eine Ventralarterie erhalten geblieben. Ich stimme Snodgrass (1938, p. 147) bei, wenn er die anderseits auch manche Spezialausbildungen aufweisenden Chilopoda als eine von den übrigen Antennaten frühzeitig abgezweigte Gruppe ansieht.

Bei allen anderen Antennaten ist also die Lage der Genitalöffnungen auf ein bestimmtes Segment fixiert. Gleichzeitig ist eine Tendenz festzustellen, die Ausmündungen der Genitalorgane nach vorn zu verlegen. Die primitivsten unter ihnen sind zweifellos die Symphyla, deren bekannte Vertreter sämtlich die Genitalöffnungen zwischen dem 3. und 4. Beinpaar haben. Von den Symphylen geht meines Erachtens ein Zweig zu den Formen mit den Geschlechtsöffnungen hinter dem 2. Beinpaar. Die hierher gehörigen Arten zeichnen sich vor allen übrigen Antennaten auch durch eine meist beträchtliche Einlagerung von Kalk in den Chitinpanzer aus. Dieser Zweig spaltet sich in die Pauropoda mit noch einem Beinpaar an jedem Segment, doch mit der ersten Anbahnung in Richtung auf eine Diplopedie an gewissen Körperstellen, sowie den so vielgestaltigen Diplopoden mit 2 Beinpaaren an den meisten Körperringen, die als Doppelsegmente aufzufassen sind. Beide Gruppen stehen sich, schon durch die Ausbildung des Gnathochilariums, zweifellos untereinander näher als eine von ihnen den Symphylen.

Ein anderer von den Symphylen abzuleitender Zweig führt zu den bereits erwähnten hexapoden Antennaten, bei denen die Geschlechtsöffnungen sekundär wieder nach hinten gerückt sind. Wie schon besprochen wurde, kann dieses Verhalten leicht mit der Abgrenzung der Segmentkomplexe ursprünglich wohl noch homonom gegliederter Körper nach Art der rezenten Symphylen und der Verlagerung der Geschlechtsorgane in das Abdomen erklärt werden. Doch ist es auch möglich, dass bei den Symphylen-artigen Ahnen die Geschlechtsöffnungen noch nicht so weit nach vorn gerückt waren als bei den Symphylen der Gegenwart. Die Art der Verwandtschaftsbeziehungen zwischen Symphylen und Apterygoten wird durch eine solche Annahme jedoch nicht beeinflusst, denn aus der grossen anatomischen Übereinstimmung zwischen Symphylen und Apterygoten kann geschlossen werden, dass die gemeinsamen Vorfahren so gestaltet waren, dass sie unbedenklich in die Gruppe der Symphyla zu rechnen sind. Ich halte es daher nicht für notwendig, die hexapoden Antennaten von einer besonderen Gruppe der Protosymphyla abzuleiten, wie das Snodgrass (1938, pp. 144, 148) tut; es ist doch selbstverständlich, dass als Ahnen nicht die Symphylen der Gegenwart in Frage kommen, die offenbar nur als einige Überlebende einer einst formenreicheren Gruppe zu werten sind.

Da die Apterygoten sowohl mit den Symphylen als auch mit den Insekten (Pterygoten) Verwandtschaftsbeziehungen haben, stellt man sie zweckmässig als besondere Gruppe zwischen beide, wie ich das bereits getan habe (Boettger, 1952, p. 273); ich sehe diese Einheiten als Klassen an. Der bei den Symphyla noch weitgehend homonome Körper gliedert sich bei den Apterygota in Zusammenhang mit der Fortbewegung auf 3 Beinpaaren in die 3 bekannten Segmentkomplexe. Bei den Insecta bilden sich an den Rückenplatten von Mesothorax und Metathorax aus Seitenlappen (Paranota) die Vorder- und Hinterflügel als dünne, flächenhaft ausgebreitete, bald in Gelenken bewegliche Hautduplikaturen, die aus 2 am Rand kontinuierlich verbundenen, aneinander haftenden Häuten bestehen und die gelegentlich durch chitinisierte Leisten verstärkt sind. Die Apterygoten laufen also auf 3 Beinpaaren; sie können nicht fliegen. Die Insekten können aber als einzige Klasse der Antennaten, ja der gesamten Protostomier, aktiv fliegen; eine Reihe von Insekten hat allerdings sekundär die Flügel wieder rückgebildet. In Abb. 1 habe ich die Verwandschaftsbeziehungen der einzelnen, von mir unterschiedenen Klassen der Antennata zusammengestellt. Es handelt sich um folgende: Chilopoda, Symphyla, Pauropoda, Diplopoda, Apterygota, Insecta.

Es muss noch ein Vorschlag von Hennig (1953, p. 64) erwähnt werden, der die als Insekten zusammengefassten hexapoden Antennaten in 2 Einheiten unterteilt, je nachdem ob bei ihnen sich die Mandibeln und 1. Maxillen in einer Kiefertasche (Atrium) befinden (Entognatha) oder aber ob die Mundteile freiliegen (Ectognatha). Dadurch werden die Apterygoten, die primär flügellosen hexapoden Antennaten, auf beide Gruppen verteilt, und zwar bilden die Diplura, Protura und Collembola die Entognatha, während die Thysanura, noch in 2 Einheiten unterteilt, mit den Pterygota in den Ectognatha zusammengestellt werden. Gegen diese systematische Gliederung wandte sich Paclt (1954), der es für richtiger hält, die bisherige Einteilung der Insekten in Apterygogenea (Apterygota) und Pterygogenea (Pterygota) einstweilen beizubehalten, bis die Frage nach einer monophyletischen Abstammung der Apterygota geklärt sei, die er noch offen lässt. Hennig (1955) wie Paclt (1956) haben dann ihre Ansichten in dieser Frage noch weiter ausgeführt. Zweifellos ist Paclt beizupflichten, wenn er der Ansicht ist, dass durch Hennigs Einteilung in Entognatha und Ectognatha eng zusammengehörige Gruppen auseinandergerissen und dass dabei die Verhältnisse im Ausbau der Mundwerkzeuge als Kriterium bei weitem überschätzt werden. Offensichtlich bilden doch die Apterygoten schon durch das Vorhandensein postadulter Häutungen und von Resten abdominaler Beinpaare, durch den Metamorphosetypus, durch die indirekte Übertragung ihrer Spermatophoren, sowie durch die primäre Flügellosigkeit innerhalb der hexapoden Antennaten untereinander eher eine systematische Einheit als die auf Grund der Lage der Mundwerkzeuge unterschiedenen Gruppen. Dennoch ist Hennig berechtigt, wegen der Ectognathie die von ihm systematisch aufgespaltenen Thysanuren den Pterygota zu nähern. Die ectognathe Lage der Mundwerkzeuge ist nämlich wohl sicher als ursprünglich anzusehen, und ihre Überwachsung durch eine Kiefertasche (Atrium)—es handelt sich nicht etwa um die Versenkung in eine solche—muss als sekundäres Merkmal gewertet werden. Deshalb können die Pterygoten aus keiner entognathen Gruppe abgeleitet werden. Nun ist aber jede systematische Abtrennung etwas Künstliches; man hat sie dort vorzunehmen, wo sie am wenigsten störend wirkt und nicht allzu nahe verwandte Formen voneinander trennt. So halte ich es für richtig, den Schnitt zwischen Thysanuren und Pterygoten (Insekten) zu legen, weil letztere zweifellos eine neue, sich stark spezialisierende Gruppe darstellen, und nicht zwischen den Thysanuren und den übrigen Apterygoten, die doch durch so viele Merkmale innig verbunden sind. Auch wirkt bei der durch Hennig auf Grund der Lage der Mundwerkzeuge vorgenommenen Einteilung der Insekten störend, dass gerade die Entognatha mit den sekundären Verhältnissen vor den Ectognatha stehen, was wegen der zahlreichen übrigen primitiven Verhältnisse erfolgt sein dürfte.

Wollte man dennoch alle hexapoden Antennaten in einer einheitlichen Klasse der Insekten vereinigen, so wäre es meines Erachtens nicht richtig, sie in 2 Unterklassen der Apterygota und Pterygota zu trennen, denn erstere umfassen weit verschiedenartigere Formen als die andere Unterklasse. Zweckmässiger ist dann die Einteilung der Insekten in 5 Unterklassen: Collembola, Protura, Diplura, Thysanura, Pterygota, wie sie beispielsweise Weber (1949) anwendet und worin ihm weitere Autoren gefolgt sind. Ich halte es jedoch aus den bereits angeführten Gründen für richtiger, die Apterygota als eine besondere Klasse der Antennaten anzuerkennen, weil sie sich durch eine beträchtliche Zahl von Besonderheiten von den Pterygota unterscheidet, denen letzteren zweckmässig allein der Name Insecta zukommt.

Innerhalb der Apterygoten sind 4 Ordnungen zu unterscheiden, die jeweils bemerkenswerte Besonderheiten aufweisen. Über Zusammenhänge unter ihnen habe ich folgende Anschauungen (hierzu Abb. 2). Da eine dieser Ordnungen, nämlich die Thysanura, noch ectognath ist, kann sie nicht von einer der übrigen, den Diplura, Protura oder Collembola, die entognath geworden sind, abgeleitet werden, weil ein solcher Vorgang doch nicht reversibel ist. Daher müssen die Thysanura sich also vom gemeinsamen Stamm der Apterygoten abgezweigt haben, als dieser noch ectognath war. In der Systematik der Apterygoten hat Grassi (1889, p. 390) dieses Merkmal erstmals verwertet, indem er innerhalb der Thysanuren, denen damals noch die jetzt als Dipluren unterschiedene Gruppe zugerechnet wurde, zwischen Entotrophi (Campodeidae, Japygidae) und Ectotrophi (Machilidae, Lepismatidae) unterschied. Dann gliederte 1891 v. Stummer-Traunfels sämtliche Apterygoten auf derselben Grundlage; doch änderte er gleichzeitig den Namen in Entognathen und Ectognathen um. Es sind das bekanntlich die Bezeichnungen, die später W. Hennig (1953, p. 64) unter Einbeziehung der Pterygoten bei der Einteilung der Insekten gebraucht hat, wobei er jedoch irrtümlicher Weise die Autorschaft der Namen v. Dalla Torre zuschrieb; dieser erwähnt aber nur die Einteilungen von Grassi (allerdings unter Zitierung einer früheren, die Einteilung noch nicht durchführenden Arbeit dieses Autors) und von v. Stummer-Traunfels in einer Fussnote und vermerkt, dass er auf die Frage nicht näher eingehen will (v. Dalla Torre, 1895, p. 4). Ebenso wie v. Stummer-Traunfels kam auch Börner (1910, pp. 638–641) zu einer Zweiteilung der Apterygoten; doch benannte er die Gruppen richtig Ectotropha und Entotropha. Ich erwähne diese Angelegenheit aus dem Grund, weil die Nomenklatur von Grassi im Sinne Börner's (1949) bei der Bearbeitung der Apterygoten im Traité de Zoologie durch Jeannel (1949, p. 13) und Denis (1949) übernommen worden ist. Wenn man nach meinem Vorschlag die Apterygota als besondere Klasse auffasst, so hätten die Ectotropha und Entotropha als Unterklassen zu gelten. Ich halte aber eine solche Unterteilung der Apterygoten in Unterklassen nicht für notwendig oder wünschenswert, weil dadurch allzusehr die Thysanuren von den ihnen doch nahe verwandten Dipluren getrennt werden. Zweckmässiger ist nach meiner Ansicht, die Klasse allein in Ordnungen zu gliedern. Doch lässt die Lage der Mundwerkzeuge bei den einzelnen Gruppen zweifellos den Schluss zu, dass sich die Vorfahren der Thysanuren bereits frühzeitig von den übrigen Apterygoten getrennt haben müssen. Noch die rezenten Arten weisen allerhand primitive Verhältnisse auf, so ausser dem Vorkommen postadulter Häutungen und der Flügellosigkeit die oft vorhandene vollständige Zahl rudimentärer oder abgewandelter Beine an einem 11–gliedrigen Abdomen, das Vorkommen von Styli an den Thoracalbeinen bei primitiven Formen (wie bei Symphylen) und die Ectognathie, wobei die Maxillentaster manchmal noch beinartig gestaltet sein können; auch die Embryonalentwicklung zeigt primitive Züge. Spezielle Bildungen der Thysanuren unter den Apterygoten sind das Vorhandensein eines medianen Terminalfilamentes am Abdomen ausser den beiden Cerci, die Unterteilung der Antennen in ein durch Muskeln bewegliches Basisglied (Scapus) und eine geringelte Geissel (Geisselantennen), deren unterstes Glied (Pedicellus) das Johnstonsche Sinnesorgan trägt, ferner die Umwandlung der 8. und 9. Abdominalbeine in Gonopoden. Die Geisselantenne mit Johnstonschem Organ hat sich erst bei den Thysanuren spezialisiert und ist von ihnen auch auf die Insekten (Pterygoten) übergegangen. Die anderen Apterygoten haben Gliederantennen, ohne Johnstonsches Organ, beibehalten, wie sie auch die übrigen Antennaten besitzen. Von den Thysanuren sind 2 Unterordnungen zu unterscheiden, in deren Benennung als Microcoryphia und Zygentoma ich mich Remington (1954) anschliesse. Die primitiveren Arten umfassen zweifellos die Microcoryphien (Fam. Machilidae und Meinertellidae), die als Sonderausbildung die springende Fortbewegungsart mit Cerci und Terminalfilament ausgebildet haben. Springen können die Zygentomen (Fam. Nicoletiidae und Lepismatidae) nicht; sie zeichnen sich aber dadurch aus, dass ihre Mandibeln mit 2 Gelenkköpfen an der Kopfplatte inserieren, wie bei den Pterygoten. Da unbestritten die Verwandtschaftsbeziehungen der Pterygoten zu den Thysanuren innerhalb der Apterygoten hinführen, hat man hauptsächlich auf Übereinstimmungen zwischen diesen beiden Gruppen geachtet, weniger auf die Tatsache, dass die Thysanuren eine grosse Zahl von hier bereits erwähnten primitiven Merkmalen aufweisen.

Die Abzweigung der Insecta (Pterygota) von den Thysanura dürfte wohl sicher nach der Trennung in Microcoryphia und Zygentoma erfolgt sein und zwar nahe der Wurzel von letzteren. In Abb. 3 sind die vermuteten Zusammenhänge dargestellt. Als primitives Erbteil haben die Insekten die Ectognathie übernommen. Die Geisselantennen und weitere Merkmale haben sie mit beiden Unterordnungen der Thysanuren gemeinsam, das doppelte Mandibelgelenk nur mit den Zygentomen. Aber bei den Thysanuren lässt sich auch bereits das Grundelement feststellen, dessen spätere Spezialisierung zu Tierformen führen sollte, die die Unterscheidung einer besonderen Tierklasse, der Insekten (Pterygoten), notwendig machte. Es handelt sich um die Ausbildung der bekannten Seitenlappen (Paranota) an den Rückenplatten der Körpersegmente; sie lassen in ihrer Struktur bei den Zygentomen schon erkennen, dass aus derartigen Gebilden am 2. und 3. Thorax-Segment sich die Insektenflügel entwickelt haben. Andeutungen von Ausbuchtungen der thoracalen Rückenplatten müssen allerdings wohl schon nahe der Wurzel der Apterygoten aufgetreten sein, denn solche finden sich auch bei manchen Dipluren (*Campodea*). Zu einer Entfaltung dieser Paranota zu Flugwerkzeugen ist es jedoch allein bei den Insekten gekommen.

Die Apterygoten-Ordnungen der Diplura, Protura und Collembola müssen nach Abzweigung der Thysanura noch eine gewisse Zeit einen einheitlichen Stamm gebildet haben, bis nämlich die ihnen gemeinsame Entognathie entstanden war, die bei ihrer Einheitlichkeit offenbar nicht mehrmals entwickelt worden ist (Abb. 2). Von diesem Stamm haben sich zweifellos zuerst die Diplura abgezweigt, denn sie zeigen noch mancherlei Übereinstimmungen mit den Thysanuren und stehen diesen sicher näher als den beiden restlichen Ordnungen, bei denen übrigens auch keinerlei Ausbuchtungen der thoracalen Rückenplatten mehr festzustellen sind. Die Dipluren tragen am 11. Abdominalsegment ein Paar faden- oder zangenartige Cerci; nicht aber besitzen sie das erst von den Thysanuren ausgebildete mediane Terminalfilament. Die 1.–7. Segmente des Abdomens besitzen bei den Dipluren noch rudimentäre Gliedmassen mit Styli und Coxalbläschen. Auch die oft 5 Ovariolen tragenden Gonaden erinnern an entsprechende Verhältnisse bei den Thysanuren, sind also wohl von einer gemeinsamen Ausgangsform abzuleiten.

Die beiden übrigen Ordnungen der Apterygoten, die Protura und die Collembola, dürften sich zuletzt voneinander getrennt und weiterhin unabhängig entwickelt haben. Die Proturen haben ein noch unverkürztes Abdomen von 11 Segmenten und einen den After tragenden Endabschnitt; sie besitzen aber nur noch 2–3 Paare von Abdominalbeinen. Mit der versteckten Lebensweise im Boden hängt es wohl zusammen, dass die Proturen die Augen verloren haben. Aber auch die Antennen sind nicht mehr vorhanden. Sie werden als Tastorgan vielleicht teilweise durch das verlängerte und erhoben getragene erste Beinpaar ersetzt, das im Gegensatz zu den hinteren beiden Beinpaaren ein Tibiotarsalgelenk besitzt und wohl auch zum Beutefang dient. Eine Sonderentwicklung der Proturen sind ferner die zu Schläuchen vereinfachten Gonaden, deren paarige Mündungen am 11. Abdominalsegment liegen; die in der Ruhe zurückgezogenen, zangenartig entwikkelten äusseren Geschlechtsorgane des Männchens dürften den Cerci homolog sein.

Eine andere Entwicklung haben die Collembolen genommen. Diese Tiere weichen offenbar am stärksten von der gemeinsamen Ausgangsform der Apterygoten ab. Ihr Abdomen erreicht zeitlebens nicht die volle Segmentzahl 11. Bei der ursprünglichen Unterordnung der Collembolen, den Arthropleona, ist noch die Segmentierung normal. Bei der anderen Unterordnung, den Symphyleona, sind die Segmente des Abdomens teilweise oder ganz verschmolzen, und das Abdomen selbst ist mehr oder weniger kugelig abgerundet. Die grosse Mannigfaltigkeit in den Sonderausbildungen der Collembolen ist hinreichend bekannt und in zahlreichen gründlichen Veröffentlichungen niedergelegt, so dass aus Zeitmangel hier darauf nicht eingegangen zu werden braucht. Auf alle Fälle sind die Collembolen diejenige Gruppe der Apterygoten, die sich am weitesten von denjenigen Formen fortentwickelt haben, die zu den pterygoten Insekten führen. Die Collembolen sind also als sehr spezialisierte Tiere einer primitiven Gruppe, der Apterygoten, anzusehen. Sie etwa wegen der manchmal geringen Zahl der Abdominalsegmente als ursprüngliche Vertreter ihrer Klasse aufzufassen, ist nach allem, was man über Spezialisierungen im Bauplan von Arthropoden weiss, nicht anzunehmen; vielmehr handelt es sich um eine sekundäre Verschmelzung von Segmenten. Durch ihre hohe Anpassungsfähigkeit haben die Collembolen die verschiedensten Biotope besiedeln können, sind in manchen Arten als einzige Vertreter der Apterygoten sogar auf die Wasseroberfläche gegangen. Das Wasser selbst wird von den Antennaten sonst nur durch manche Insekten (Pterygoten) in verschiedenen Stadien sekundär besiedelt. Die bekannten ursprünglichen Antennaten sind aber sämtlich Landtiere, alle mit Stigmenatmung. Trotzdem müssen die Vorfahren der Antennaten aus dem Wasser stammen, denn ihre nächsten Verwandten sind die Crustaceen, die im Wasser verblieben sind, dort ihre hauptsächliche Entwicklung genommen und in Zusammenhang mit der freischwimmenden Lebensweise den Spaltfuss herausgebildet haben. Uber die an der Basis beider Gruppen anzunehmenden Verwandtschaftsbeziehungen zwischen Antennaten und Crustaceen ist mehrfach berichtet worden. Es darf noch erwähnt werden, dass die Exemplare einer gemeinsamen Ausgangsform wie die Crustaceen "Diantennaten" gewesen sein müssen. Das zweite Antennenpaar ist zwar bei den Antennaten zurückgebildet worden; doch sind die sie einst innervierenden Ganglien noch als tritocerebrale Lappen nachweisbarr (Snodgrass, 1938, p. 140).

Die Differenzierung der einzelnen Ordnungen der Apterygoten muss bereits in geologisch sehr früher Zeit erfolgt sein, denn Collembolen hat man bekanntlich schon in Ablagerungen des mittleren Devons gefunden (Hirst and Maulik, 1926; Tillyard, 1928; Scourfield, 1940). Auf Grund dieses Fundes ist man aber nicht etwa berechtigt, die Collembolen als Stammform der Klasse anzusehen und von ihnen die übrigen Gruppen abzuleiten, denn allgemein sind fossile Apterygoten nur sehr lückenhaft erhalten geblieben. Funde aus dem Carbon, die man zunächst als Thysanuren angesehen hatte, haben sich bei kritischer Prüfung als Angehörige anderer Arthropoden-Gruppen, nicht als Apterygoten, erwiesen. Doch kennt man aus der Trias einen Vertreter der Thysanuren, nämlich *Triassomachilis uralensis* Sharov; für ihn ist die Aufstellung einer besonderen Fam. Triassomachilidae nötig, die C. L. Remington (1954, pp. 280, 282–283) zu den Microcoryphia stellt. Weiter hat man eine zu den Collembolen zu rechnende Art in dem sogenannten Chemawinit festgestellt, dem kanadischen Bernstein, der in die oberste Kreide eingestuft wird (Carpenter, 1937; Folsom, 1937). Im Tertiär (baltischer Bernstein) sind dann Thysanuren (Silvestri, 1912; v. Olfers, 1912), Dipluren (Silvestri, 1912, pp. 45–46) und Collembolen (Handschin, 1926) vertreten. Allerdings gehört die zunächst zu den Dipluren gestellte *Ocellia articulicornis* v. Olfers aus dem baltischen Bernstein (v. Olfers, 1907, pp. 7–8) nicht zu dieser Gruppe, sondern offenbar zu den Dermapteren (Silvestri, 1912, pp. 43, 65; Handlirsch, 1925, pp. 221; Wygodzinsky, 1943, pp. 519).

LITERATURVERZEICHNIS

Börner, C. 1910. Die phylogenetische Bedeutung der Protura. *Biolog. Centralbl.* 30: 633–641.

Boettger, C. R. 1952. Die Stämme des Tierreichs in ihrer systematischen Gliederung. *Abhandl. Braunschweig. Wissensch.* Ges. 4: 238–300.

Carpenter, F. M. 1937. Introduction. *In:* Insects and arachnids from Canadian amber. *Univers. Toronto Stud. Geolog. Ser.* 40: 7–13.

v. Dalla Torre, K. W. 1895. Die Gattungen und Arten der Apterygogenea (Brauer). *Programm Staats-Gymn. Innsbruck* 46: 3–23.

Denis, R. 1949. Sous-classe des Aptérygotes (Apterygogenea, Brauer, 1885, Apterygota, Lang, 1889). Anatomie —Biologie—Systématique. *In:* P. P. Grassé, *Traité de Zoologie* 9: 111–275.

Folsom, J. W. 1937. Insecta, order Collembola. *In:* Insects and arachnids from Canadian amber. *Univers. Toronto Stud. Geolog. Ser.* 40: 14–17.

Grassi, B. 1889. Les ancêtres des myriapodes et des insectes. Anatomie comparée des thysanoures et considérations générales sur l'organisation des insectes. *Arch. Ital. Biolog* 11: 1–11, 291–337, 389–419.

Handlirsch, A. 1925. Palaeontologie. *In:* C. Schröder, Handbuch der Entomologie 3: 117–306. Jena.

Handschin, E. 1926. Revision der Collembolen des baltischen Bernsteins. *Entomol. Mitteil.* 15: 161–185, 211–223, 330–342.

Handschin, E. 1926. Über Bernsteincollembolen. Ein Beitrag zur ökologischen Tiergeographie. *Rev. Suisse Zoolog.* 33: 375–378.

Handschin, E. 1952. Die Bedeutung der postembryonalen Entwicklung für die Protomorpha (Collembolen). *Transact. IX. Intern. Congr. Entomol.* 1: 235–240.

Hennig, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. *Beitr. Entomol.* 3, Sonderheft: 1–85.

Hennig, W. 1955. Meinungsverschiedenheiten über das System der niederen Insekten. *Zool. Anzeig.* 155: 21–30.

Hirst, S., and S. Maulik. 1926. On some Arthropod remains from the Rhynie Chert (Old Red Sandstone). *Geolog. Magaz.* 63: 69–71.

Jeannel, R. 1949. Les insectes. Classification et phylogénie, les insectes fossiles, évolution et géonémie. *In:* P. P. Grassé, *Traité de Zoologie* 9: 1–110.

v. Olfers, E. W. M. 1907. Die "Ur-Insekten" (Thysanura und Collembola im Bernstein). *Schrift. Physik.-ökonom. Ges. Königsberg i.Pr.* 48: 1–40.

v. Olfers, E. W. M. 1912. Ein neuer Thysanur im Bernstein. *Berlin. Entomol. Zeitschr.* 56: 151–152.

Paclt, J. 1954. Zum phylogenetischen System der niederen Insekten. *Zool. Anzeig.* 153: 275–281.

Paclt, J. 1956. Nochmals über das System der niederen Insekten. *Zool. Anzeig.* 156: 272–276.

Remington, C. L. 1954. The suprageneric classification of the order Thysanura (Insecta). *Ann. Entomol. Soc. America* 47: 277–286.

Scourfield, D. J. 1940. The oldest known fossil insect (*Rhyniella praecursor* Hirst and Maulik)—further details from additional specimens. *Proc. Linn. Soc. London* 152: 113–131.

Silvestri, F. 1912. Die Thysanuren des baltischen Bernsteins. *Schrift. Physik.-ökonom. Ges. Königsberg i.Pr.* 53: 42–66.

Snodgrass, R. E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithson. Miscell. Collect.* 97, No. 6.

Ritter v. Stummer-Traunfels, R. 1891. Vergleichende Untersuchungen über die Mundwerkzeuge der Thysanuren und Collembolen. *Sitzungsber. Kais. Akad. Wissensch. Wien, Mathem. Naturwiss.* Cl. 100, Abth. 1: 216–235.

Tillyard, R. J. 1928. Some remarks on the Devonian fossil insects from the Rhynie Chert Beds, Old Red Sandstone. *Trans. Entomol. Soc. London* 76: 65–71.

Verhoeff, K. W. 1910–14. Die Diplopoden Deutschlands. Leipzig.

Weber, H. 1949. Grundriss der Insektenkunde. 2. Aufl. Jena.

Wygodzinsky, P. 1943. Note on the origin and classification of Apterygota. *Revist. Entomol.* 14: 516–521.

L'Appareil buccal de *Chrysochroma bipunctatum* Scop. (Dipt. Stratiom.)

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RÉSUMÉ

L'appareil buccal de Chrysochroma bipunctatum *(sous-famille des Geosarginae) est étudié comparativement à celui d'*Eulalia *(Gouin, 1950). Ses caractères les plus remarquables sont la jointure rigide du sclérite central du clypéus ("centroclypéus", Gouin, 1949) au crâne et la soudure des extrémités antérieures du centroclypéus et du fulcrum avec la base des stylets impairs de la trompe (labroépipharynx et hypopharynx). Cette double soudure donne à l'appareil buccal de* Chrysochroma *sa rigidité, alors que celui d'*Eulalia*, n'ayant pas ces connexions, est mobile et la trompe rétractile, rappelant le fonctionnement de la trompe cyclorrhaphe. La séparation systématique des deux genres est corroborée par la morphologie, qui est le fondement de la taxinomie et de toute théorie phylogénique. (cf. Gouin, 1957).*

L'appareil buccal de *Chrysochroma bipunctatum* (sous-famille des Geosarginae) diffère sensiblement de celui d'*Eulalia sp.* (Gouin, 1950), représentant de la sous-famille des Stratiomyinae. En voici les traits essentiels.

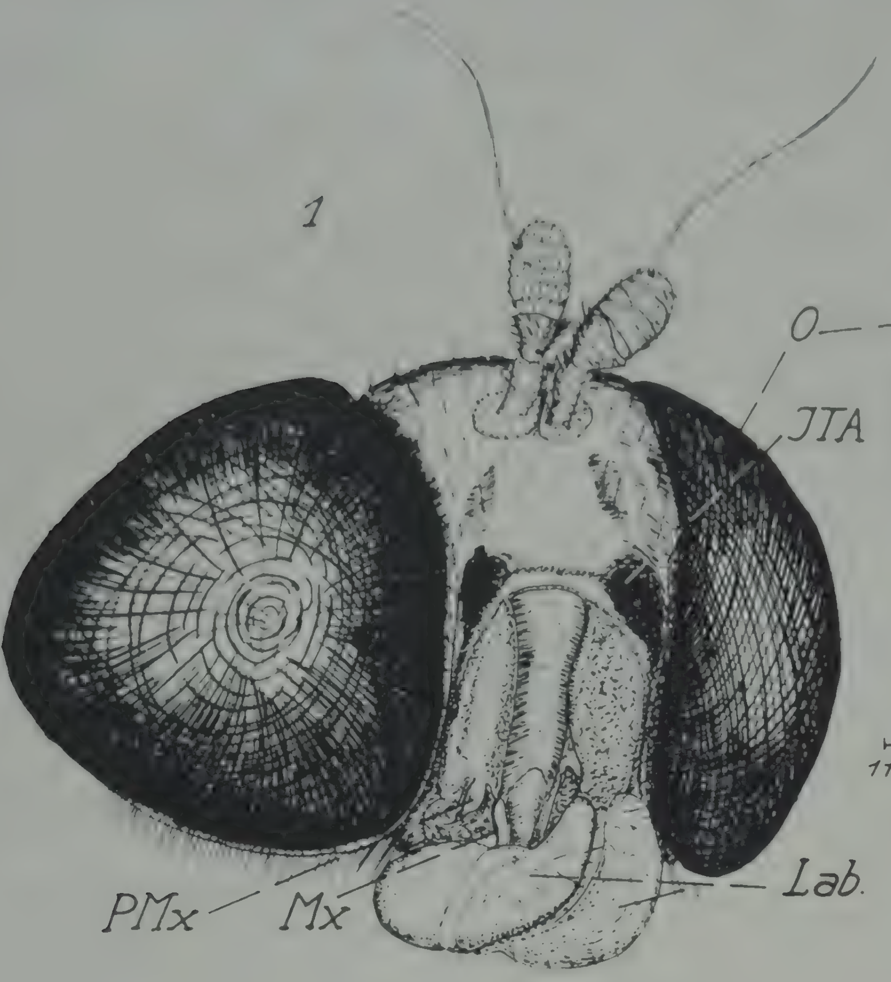
Comme chez de nombreux Brachycères, la tête (Figs. 1 et 2) est très mobile et pivote autour des sclérites nucaux et sur le prothorax. Le foramen s'ouvre au centre de la concavité; la gula est assez sclérifiée du côté du foramen, moins du côté de la trompe. La face, mise à part l'aire clypéale membraneuse, ne présente pas de particularités.

L'appareil buccal (Fig. 3) est constitué par les parties habituelles (Gouin, 1949, p. 250): la trompe et le rostre. Le corps labial est très court, mais les labelles (Figs. 2, 3, 5) passablement développés. Ils sont peu sclérifiés, car à peine y distingue-t-on les sclérites d'insertions musculaires s'articulant dans une large échancrure antérieure du prémentum. Ils présentent extérieurement les traces d'une segmentation, mais la surface interne des labelles d'un même côté est indivise et sillonnée de pseudotrachées parallèles aboutissant toutes à une large gouttière longeant le bord interne des labelles; la fermeture et la solidarité des deux systèmes pseudotrachéaux symétriques sont assurées par une sorte d'engrenage. Le court prémentum est peu et incomplètement sclérifié, de structure nettement paire; il est relié à la région gulaire de la tête par une membrane, qui ne lui donne qu'une très faible mobilité longitudinale. La musculature labiale est conforme au plan d'organisation orthorrhaphe (Gouin, 1949, 257 sq.). Le labro-épipharynx et l'hypopharynx lamellaire, très courts et assez sclérifiés, ne présentent pas de particularités notables. (Fig. 4).

La maxille (Figs. 1, 3, 4) est sans conteste l'organe le plus remarquable de tout l'appareil buccal. Très petits, les éléments constitutifs se reconnaissent à peine, la lacinia est réduite à une lame flexible située hors de la trompe et adjacente latéralement au labro-épipharynx. Le palpe, à peine visible au milieu de la partie membraneuse du clypéus, tend à perdre son insertion sur le stipes. Un seul muscle est bien développé: son origine se trouvant sur le tentorium, il représente le muscle tentorio-stipital.

Les éléments cibariaux de l'appareil buccal, formant le rostre, sont représentés par un fulcrum large et évasé et par le sclérite médian du clypéus ("centroclypéus", Gouin, 1949, p. 253), fortement sclérifié, bombé et rétréci, rigidement articulé au front par un joint membraneux extrêmement étroit. Les parties antérieures du centroclypéus et du fulcrum sont soudées à la base des stylets impairs de la trompe. Ces connexions donnent à la trompe et au rostre une très grande rigidité.

La cavité cibariale du fulcrum se continue dans l'ampoule de la pompe pharyngienne antérieure. C'est dans l'étroit espace formé par le dernier faisceau des dilatateurs cibariaux, la paroi céphalique, l'ampoule pharyngienne et le fulcrum que se trouve le ganglion frontal, important repère, qui délimite, selon Snodgrass, les domaines cibariaux et frontaux. Cette pompe pharyngienne est mue par deux paires de puissants muscles de direction perpendiculaire; la paire antérieure a son origine près du bord clypéal du front, tandis que la paire postérieure prend appui sur une carène interne près de l'insertion des antennes, alors que chez *Tabanus* ce muscle se fixe très près des ocelles. Le troisième muscle est un muscle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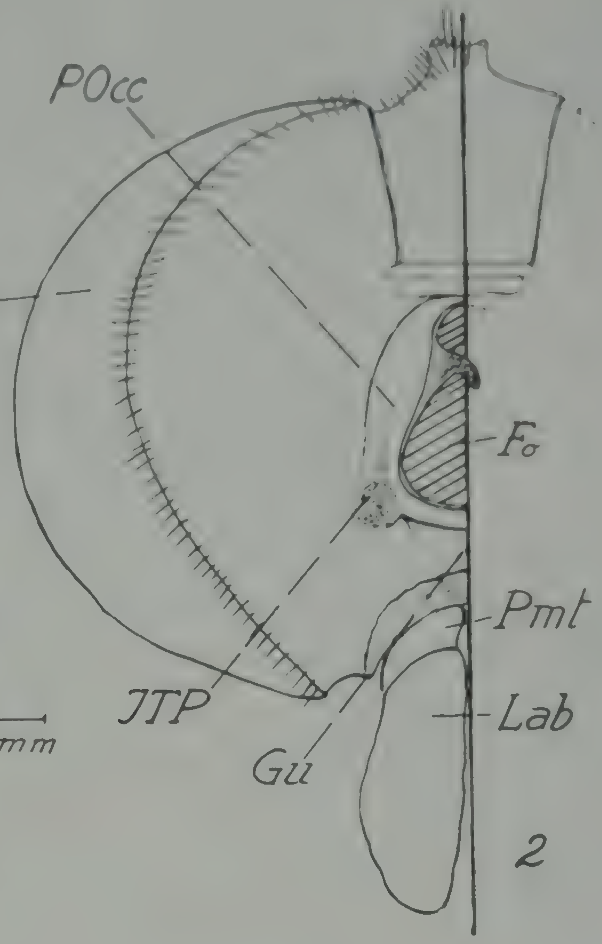
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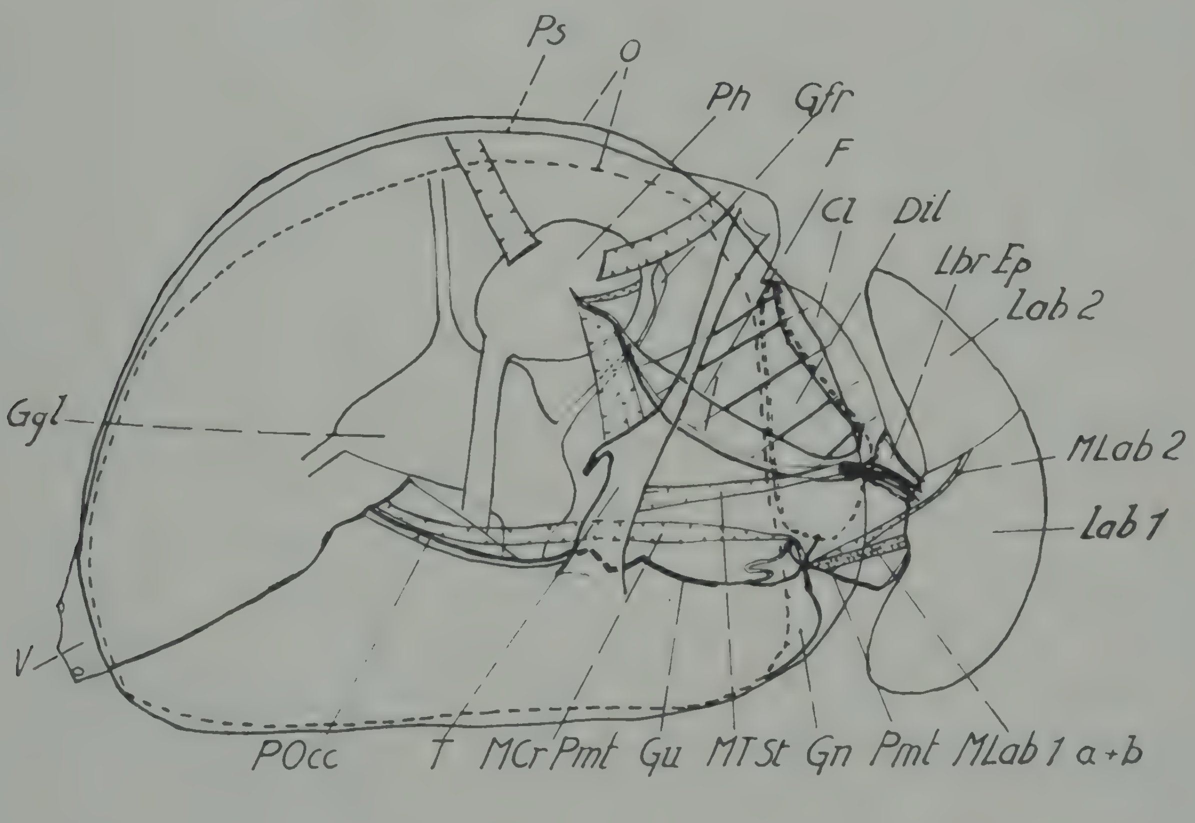
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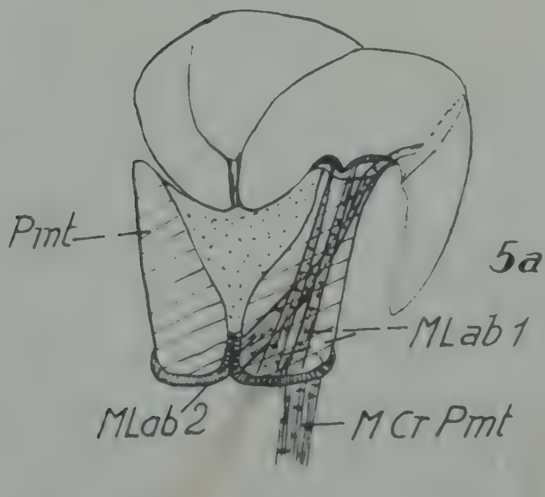
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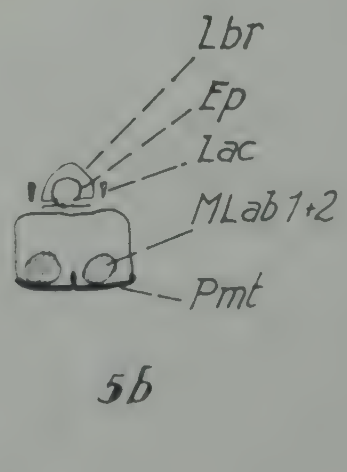
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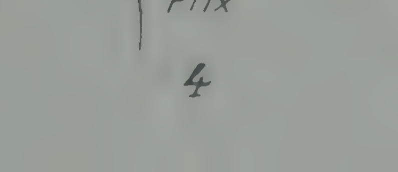
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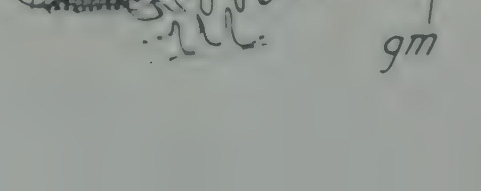
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circulaire allant d'une corne fulcrale à l'autre. A la sortie de l'ampoule pharyngienne, le tube digestif pénètre dans le ganglion cérébroïde et se dirige directement vers le foramen.

Cet appareil buccal présente de notables différences avec celui d'*Eulalia sp*. Elles tiennent toutes dans les connexions corrélatives avec deux modes de fonctionnement (Gouin, 1949, p. 253–4): la rigidité et l'immobilité du rostre et de la trompe de *Chrysochroma*, qui est la manière d'être primitive, d'une part, et d'autre part, chez *Eulalia*, la protractilité et la rétractilité, faibles, il est vrai, des mêmes organes qui, apparaissent çà et là chez les Orthorrhaphes (*Bombylius*, par exemple, mais non chez *Asilus*), préfigurent en quelque sorte le mode de fonctionnement normal, mais combien plus perfectionné, du même appareil chez les Cyclorrhaphes.

Les genres *Eulalia* et *Chrysochroma* sont placés par les systématiciens (Séguy, Lindner) dans deux sous-familles différentes: cette séparation est corroborée par la morphologie des appareils buccaux des imagos. C'est un nouvel exemple de l'appui que fournit à la systématique l'anatomie comparée, fondement le plus sûr de la taxinomie et de toute théorie phylogénique (Gouin, 1957).

BIBLIOGRAPHIE

Gouin, F. 1949. Recherches morphologiques sur l'appareil buccal des Diptères. *Mém. Mus. Nat. Hist. Nat.*, Paris, 28(4): 167–269.

Gouin, F. 1950. L'appareil buccal d'*Eulalia sp. Bull. Soc. Ent. France* 55(2): 22–26.

Gouin, F. 1957. Etudes sur l'anatomie de la tête larvaire de quelques Chironomidae (Dipt. Nematoc.). *Ann. Soc. Entomol. France* 126: 105–138.

Fig. 1. Tête, vue de trois-quarts. ITA, invagination tentoriale antérieure. Lab, premier et deuxièmes labelles. O, oeil. PMx, palpe maxillaire; à côté apparaît la lacinia (Mx).

Fig. 2. Paroi postérieure de la tête. Fo, foramen. Gu, gula. ITP, invagination tentoriale postérieure. Pmt, prémentum. POcc, postocciput.

Fig. 3. Diagramme de l'appareil buccal. PS, tracé de la coupe sagittale. O, tracé de la plus grande extension de l'oeil (en trait plein) et de l'orbite (en trait interrompu). Ph, pharynx et ses muscles. Gfr, ganglion frontal. F, fulcrum et muscles. Cl, centro-clypéus; en pointillé double le contour de l'aire clypéale membraneuse. Dil, muscles dilatateurs cibariaux de la cavité fulcrale. LbrEp, labroépipharynx; en-dessous, la lacinia et l'hypopharynx. Lab 2, deuxième labelle. MLab, 2 son muscle. Lab 1, premier labelle. MLab la + b, ses deux muscles antagonistes. Gn, genae. MTSt, muscle tentoriostipital. MCrPmt, muscle cranioprémental. T, tentorium. POcc, postocciput. V, vertex. Ggl, ganglion cérébroïde. Antenne non figurée.

Fig. 4. Détails des connexions entre le clypéus, le fulcrum, le labroépipharynx, l'hypopharynx et la maxille. Adossée au fulcrum, la soupape salivaire et le muscle "grêle". Lettres comme à la Fig. 3.

Fig. 5. Détails du labium: a) éléments constitutifs; b) coupe schématique de la trompe montrant la disposition des éléments; c) structure des deux labelles d'un même côté. Pstr, réseau des pseudotrachées débouchant dans une gouttière médiane (gm); plus intérieurement, la membrane festonnée dorsale s'engrenant avec sa symétrique. Autres lettres comme aux figures précédentes.

Ontogenèse de l'Organe de Johnston chez divers Insectes

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RÉSUMÉ

La présente communication expose les résultats de recherches anatomiques sur l'antenne du Termite, Calotermes flavicollis, *et de deux Phasmides,* Carausius morosus *et* Sipyloidea sipylus. *Les méthodes utilisée sont la coloration supra vitale au bleu de méthylène et les colorations triples sur coupes. On étudie la morphologie de l'organe de Johnston chez la larve néonate et on montre ses variations au cours des mues successives. En particulier, on met en évidence l'évolution des terminaisons nerveuses au moment du rejet de la cuticule; le filament distal, très long, qui rattache le clou scolopal à la cuticule, est rejeté et régénéré. Ce rejet ne semble pas se produire pour d'autres organes chordotonaux antennaires. L'augmentation du nombre de clous scolopaux au cours de l'ontogénèse est assez faible, mais certaines figures laissent à penser qu'elle est due à un dédoublement des éléments nerveux.*

INTRODUCTION

Ces recherches anatomiques ont été effectuées par nous sur les antennes d'un Termite, *Calotermes flavicollis* Fab. et par notre élève, Madame Urvoy, sur les antennes de deux Phasmes, *Carausius* (*Dixippus*) *morosus* Brunner et *Sipyloidea sipylus* Westwood. Après avoir donné la description de l'innervation générale du pédicelle antennaire, nous montrons comment varie l'organe de Johnston au cours de l'ontogénèse: son plan d'ensemble reste le même; seul varie le nombre de clous scolopaux formant l'organe. Nous avons pu donner quelques précisions sur la manière dont se produit l'augmentation du nombre de clous scolopaux à la mue et nous rapprochons l'organe de Johnston des sensilles externes du point de vue de son comportement au cours de la mue.

MÉTHODES

Nous avons coloré les nerfs et les terminaisons nerveuses soit *in toto* par injections de bleu de méthylène Gurr dans l'animal vivant, soit sur coupes en utilisant la triple coloration de Prenant modifiée par Badonnel (1934). La première méthode, déjà décrite par Richard (1950) donne d'excellents résultats de topographie générale; la seconde permet de préciser quelques données cytologiques.

Nous avons étudié dans tous les cas la structure de l'organe de Johnston de la larve néonate, puis l'évolution de cette structure au cours des mues successives jusqu'au stade imaginal.

RÉSULTATS

Comme chez tous les Insectes, l'organe de Johnston se situe dans le pédicelle antennaire. Il présente à peu près la même structure chez le Termite et chez les Phasmes.

Les nerfs antennaires issus des deux lobes antennaires des ganglions cérébroïdes se divisent en deux branches dans le scape peu avant d'entrer dans le pédicelle. Les deux branches sont l'une antérieure, l'autre postérieure dans l'antenne et elles vont se terminer dans l'article distal. En traversant le pédicelle, ces deux branches innervent les nombreuses soies sensorielles et les deux complexes chordotonaux qui occupent l'article:

a—l'organe chordotonal du pédicelle proprement dit. Ses cellules forment une masse compacte relativement importante chez le Termite, bien plus volumineuse chez les Phasmes où les cellules sont enrobées dans de nombreuses fibres (Figs. 3 et 4). Chez le Termite, cet organe reçoit son innervation d'une branche du nerf antérieur et les clous scolopaux vont s'attacher à la paroi distale du pédicelle après un trajet oblique latéro-antérieur. L'organe adulte comprend une douzaine de clous scolopaux desquels on obtient facilement des préparations très lisibles. Chez les Phasmes, cet organe, qui comporte environ vingt clous chez l'adulte, est innervé par deux petits rameaux détachés des gros troncs issus des nerfs antérieur et postérieur; chacun des deux rameaux innerve à peu près la moitié de l'organe et les clous vont s'attacher ensemble à la face ventrale du pédicelle, au niveau d'un renforcement de la cuticule.

b—l'organe de Johnston. Il est constitué par un grand nombre de clous scolopaux tangentiels à la cuticule. Chez les Termites comme chez les Phasmes, chacune des deux branches nerveuses du pédicelle fournit un nerf de Johnston qui dessert une moitié des clous scolopaux de l'organe. L'ensemble des clous forme une couronne qu'on voit aussi bien chez les Phasmes que chez les Termites, contrairement à l'avis émis par Eva Borchardt (1927).

La terminaison des clous scolopaux sur la cuticule est différente chez les Termites et chez les Phasmes. Pour les premiers, le filament terminal se recourbe à son extrémité, avant de venir s'attacher à la cuticule, au niveau d'un très faible renforcement de celle-ci. L'insertion se fait dans la région articulaire souple, entre le pédicelle et le troisième article. Chez les Phasmes, le filament terminal ne se recourbe pas et vient s'insérer sur la cuticule, au niveau d'un cône fortement marqué et ressemblant aux "knobs" décrits par Vowles (1954) chez les Fourmis et par MacIndoo (1922) chez l'Abeille. Le cône est une dépendance de la cuticule épaisse de l'extrémité distale du pédicelle et n'appartient pas à la membrane arthrodiale, contrairement à ce qu'on a parfois prétendu.

L'organe de Johnston existe déjà chez la larve néonate des Termites comme des Phasmes. Son plan d'ensemble reste le même pendant toute la croissance. Seul change le nombre des clous scolopaux de la couronne. Chez le *Calotermes flavicollis*, on compte 15 à 17 clous dans l'antenne de la larve du premier stade de développement. Aux 2° et 3° stades, on compte une vingtaine de clous; au 4° stade, 25 clous; aux stades 5 à 7, 30 à 35 clous; enfin, les imagos possèdent 40 clous scolopaux. Ches les Phasmes, on peut mettre en évidence une augmentation de 5 à 6 clous scolopaux à chaque stade, entre les valeurs 24 pour le 1° stade et 70 pour l'adulte. (36 au 3° stade; 42 au 4° stade).

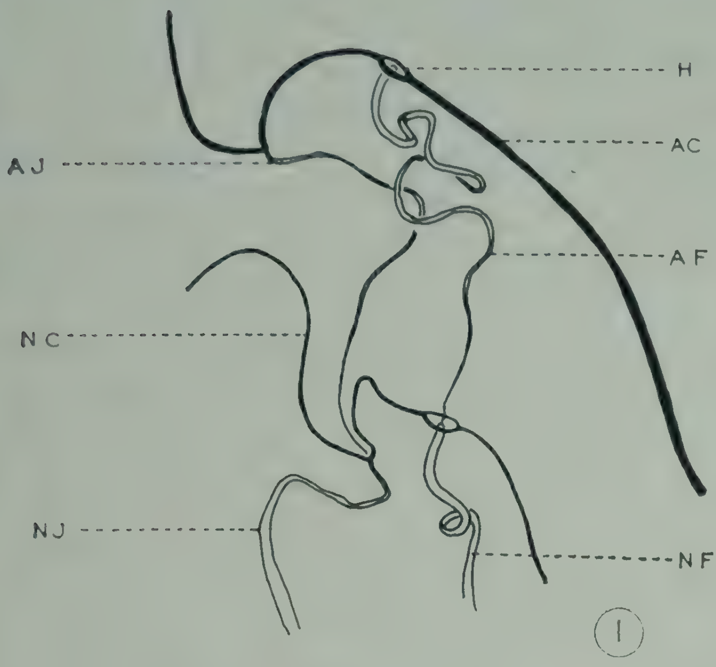
Il n'y a aucune augmentation brusque importante, soit au cours des derniers stades larvaires, soit à la mue imaginale. Il est même assez difficile de trouver une figure nette d'augmentation du nombre de clous scolopaux, au cours des mues. Néanmoins, chez une larve de *Calotermes* en cinquième mue (passage du 5° au 6° stades de développement), nous avons pu observer deux cellules nerveuses accolées prolongées par deux terminaisons étroitement serrées l'une contre l'autre, particulièrement au niveau des clous scolopaux. Les filaments distaux avaient des insertions proches mais distinctes, qui correspondaient à une seule insertion sur l'ancienne cuticule (Fig. 2). Nous pensons donc que la multiplication des clous scolopaux se fait par duplication des terminaisons nerveuses préexistantes, duplication qui s'opère au moment de la préparation de la mue. Ceci rejoint d'ailleurs ce que nous avons déjà montré pour d'autres sensilles de *Calotermes* (Richard 1952).

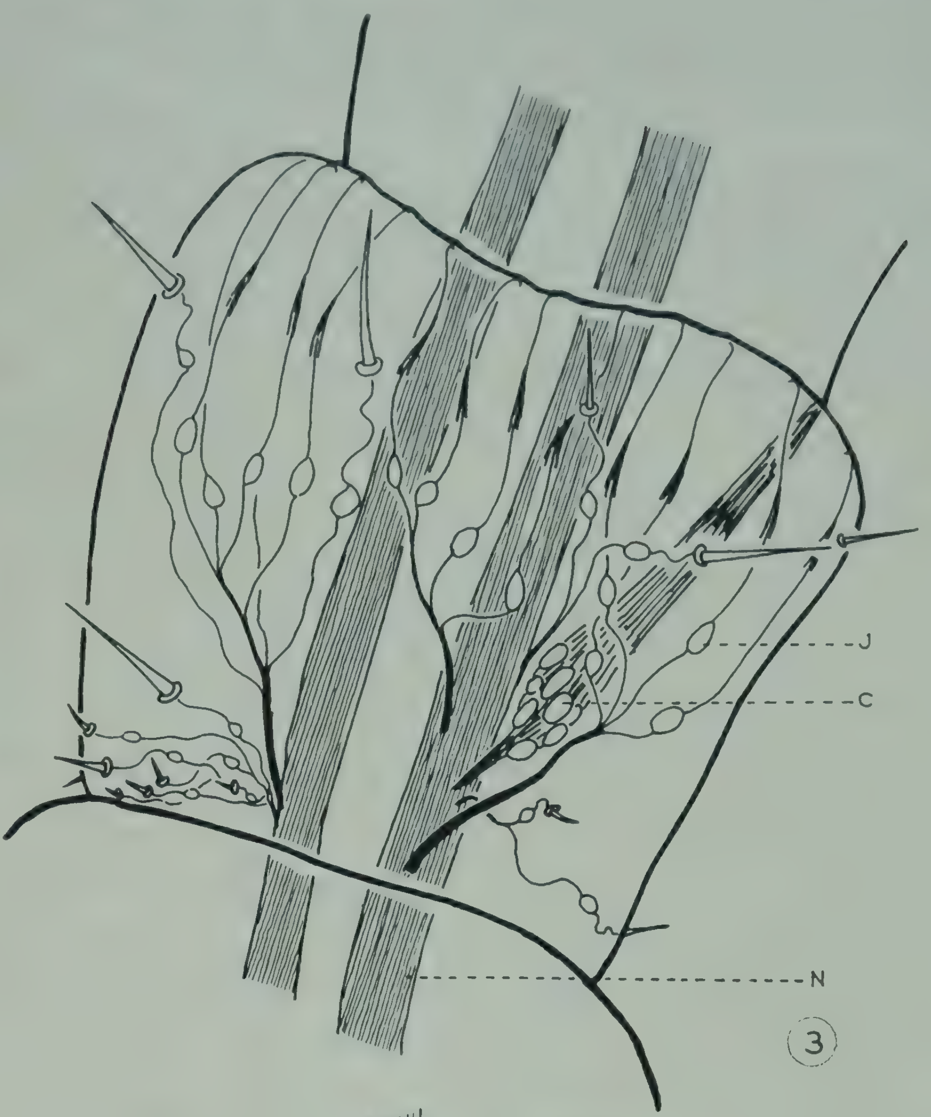
Lorsqu'on étudie de près les processus d'exuviation, on s'aperçoit que l'organe de Johnston présente un certain nombre de caractères particuliers. Les longs filaments distaux, décrits plus haut, se coupent quelque temps avant la mue et sont rejetés avec l'exuvie; de nouveaux filaments ont régénéré auparavent et s'attachent sur la nouvelle cuticule (Fig. 1). Ceci rappelle de très près ce qui se passe pour les autres sensilles, sensilla trichodea en particulier (Richard 1952, Denis 1956). Par contre, l'organe chordotonal du pédicelle passe en bloc, filaments terminaux compris, de l'ancienne à la nouvelle cuticule: on ne remarque sur l'ancienne cuticule au niveau de son insertion, qu'une série de très petits points colorables par le bleu de méthylène, mais qui n'ont rien de comparable avec les filaments que laissent l'organe de Johnston et les autres sensilles.

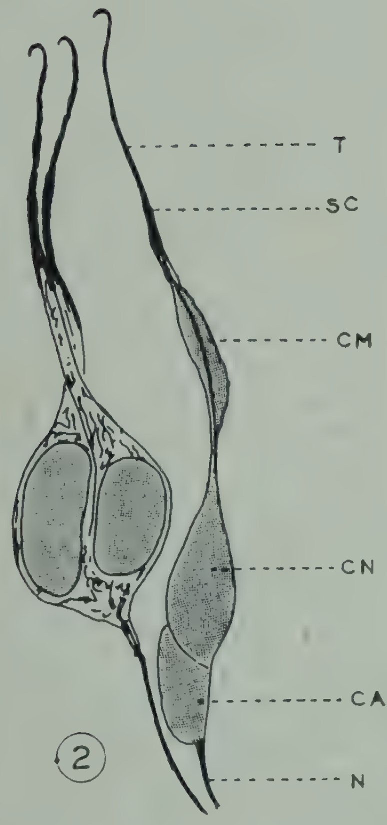
Dans les cas de coupure d'antenne chez les Phasmes, les régénérats obtenus après section dans le pédicelle prennent la forme d'une extrémité de patte et l'organe de Johnston ne régénère pas, bien que le plan d'ensemble de l'innervation, à la base du régénérat, soit celui d'une antenne.

Cette étude ontogénétique, destinée à donner une base anatomique à quelques expériences de physiologie, nous a permis de poser quelques problèmes et d'établir des comparaisons.

Etudiés à la lumière des recherches de Debauche (1936), ces organes de Johnston montrent quelques caractères primitifs; en particulier, le fait que les scolopidia ne soient pas groupés en scoloparia bien distincts. Mais, si chez les Phasmes, on peut voir encore à la fois des clous scolopaux et des pores de Hicks nombreux (une vingtaine au 4° stade) sur le pédicelle antennaire, ces derniers disparaissent presque chez le Termite: 4 à 6 chez l'imago. En même temps, les clous de l'organe chordotonal du pédicelle sont moins nombreux chez le Termite que chez les Phasmes. Tout ceci confirme les conclusions de Debauche.







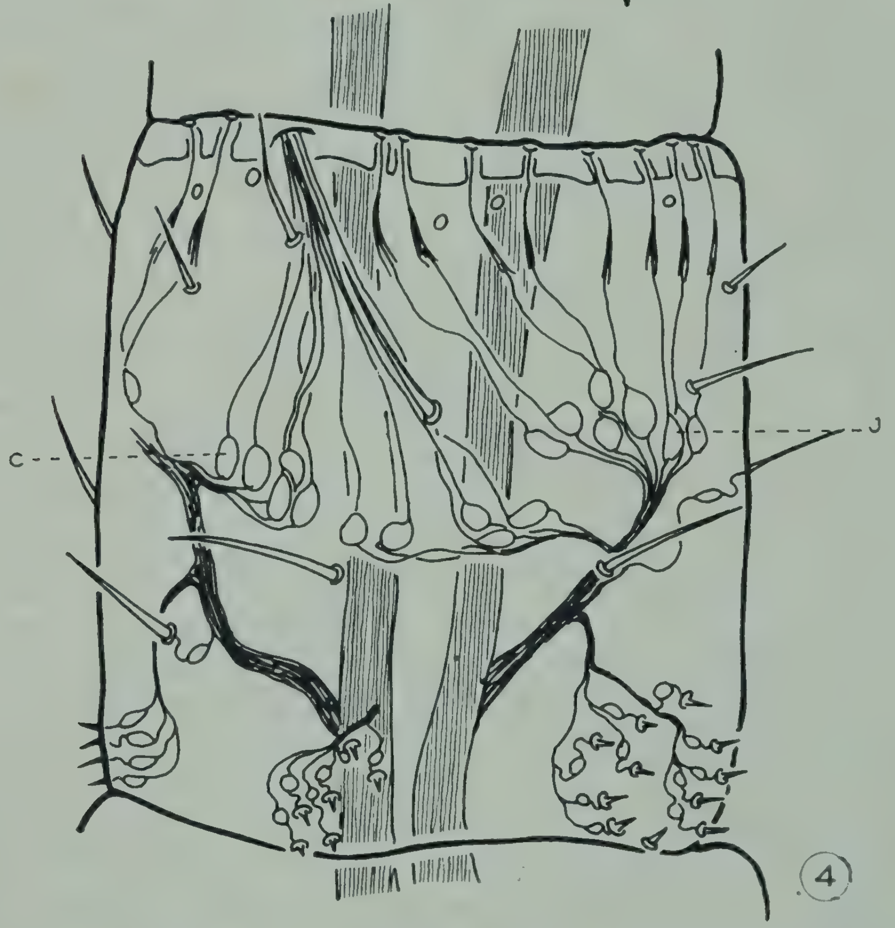


Fig. 1. Terminaisons sensorielles en cours d'exuviation chez une larve de *Calotermes flavicollis*. AC, ancienne cuticule; AF, ancien filament terminal innervant un pore de Hicks; AJ, ancien filament terminal d'un clou scolopal de l'organe de Johnston; H, pore de Hicks; NC, nouvelle cuticule; NF, nouveau filament terminal innervant le pore de Hicks; NJ, nouveau filament terminal du clou scolopal de l'organe de Johnston.

Fig. 2. Duplication de terminaisons nerveuses sensorielles. A gauche, terminaison double; à droite, terminaison simple. CA, cellule accessoire; CM, cellule moyenne; CN, cellule nerveuse; N, filet nerveux proximal; SC, corps scolopal; T, filament terminal du clou scolopal.

Figs. 3–4. Pédicelle antennaire. 3, nymphe de *Calotermes flavicollis* Fab. au 7° stade de développement. 4, larve de *Sipyloidea sipylus* Westwood au premier stade de son développement. C, cellules nerveuses de l'organe chordotonal du pédicelle; J, cellules nerveuses de l'organe de Johnston; N, branche antérieure du nerf antennaire. On n'a pas représenté l'innervation de toutes les sensilles externes pour simplifier la figure.

Par contre, nous pensons que l'organe décrit par Eva Borchardt (1927) comme organe de Johnston, n'est autre que l'organe chordotonal du pédicelle; son affirmation selon laquelle *Dixippus morosus* ne posséderait pas d'organe de Johnston circulaire comme les autres Insectes, est fausse. Ceci d'ailleurs ne met pas en cause la question de savoir si l'organe de

Johnston joue un rôle dans la régénération antennaire puisque la section du pédicelle entraîne l'ablation simultanée des deux groupes d'organes. Les expériences en cours dans mon Laboratoire apporteront peut-être bientôt quelques précisions à ce sujet.

Comme Snodgrass (1935), nous pensons que l'organe de Johnston n'a pas exactement la même nature que les autres organes chordotonaux puisqu'anatomiquement et par son comportement au cours des mues, il se rapproche plus des sensilla trichodea que des clous scolopaux normaux.

Au moment où l'on s'accorde, en général, pour attribuer à l'organe de Johnston un rôle important dans la perception des ébranlements mécaniques voire même du géotropisme, il nous a semblé important de démontrer d'une part que cet organe se compose de deux moitiés symétriques susceptibles de fournir à l'Insecte des indications sur les déformations de la cuticule des deux faces de l'antenne et, d'autre part, qu'il ne varie pas de structure mais seulement d'importance au cours du développement de l'Insecte, ce qui laisse à penser que, à des degrés près, le fonctionnement de cet organe est le même à tous les stades de la vie larvaire ou imaginale.

BIBLIOGRAPHIE

Badonnel, A. 1934. Recherches sur l'anatomie des Psoques. *Bull. biol. France Belg. Suppl.* 18.

Borchardt, E. 1927. Beitrag zur heteromorphen regeneration bei *Dixippus morosus*. *Roux Arch. J. Entwickl. Organisms* 110.

Debauche, H. 1936. Etude cytologique et comparée de l'organe de Johnston des Insectes. *La Cellule* 45.

Denis, C. 1956. Contribution à l'étude topographique et cytologique des sensilles externes des pattes de *Calotermes flavicollis* Fab. au cours de l'ontogénèse sensorinerveuse. *Ins. Sociaux* (Sous presse).

De Wilde, J. 1941. Contribution to the physiology of the Johnston organ and its part on the behaviour of the *Gyrinus*. *Arch. Neerland. physiol.* 25.

Johnston, A. 1855. Auditory apparatus in the *Culex* mosquito. *Quart. J. Microsc. Sci.* 3.

MacIndoo, I. 1922. The auditory sense of the honey bee. *J. Comp. Neurol.* 34.

Richard, G. 1950. Le phototropisme des Termites en rapport avec leur anatomie sensorielle. *Ann. Sci. Nat.*, 11° série, 12.

Richard, G. 1952. Innervation sensorielle pendant les mues chez les Insectes. *Bull. Soc. Zool.* France 77.

Richard, G. 1956. Contribution à l'étude du géotropisme de *Calotermes flavicollis* Fab. *J. Psych.* 53.

Snodgrass, R. E. 1935. Principles of insect morphology. *McGraw-Hill Book Co.*, New York, London.

Urvoy, J. 1956. Contribution à l'étude de l'ontogenèse de l'organe de Johnston chez les Phasmides. *Bull. Soc. Scient. Bretagne.* (Sous presse).

Vowles, D. M. 1954. The orientation of ants. Orientation to light, gravity and polarized light. *J. Exp. Biol.* 31.

Contributions to the Anatomy of *Grylloblatta campodeiformis* Walker[1]

6. The Nervous System

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ABSTRACT

This paper is a contribution to Professor E. M. Walker's existing monographs on the anatomy of Grylloblatta campodeiformis. *In it is described in detail the gross anatomy of the supra-oesophageal ganglion, the ventral ganglionic chain, and the stomatogastric system. Comparisons are made with the nervous systems of related orthopteroid insects and an attempt is made to correlate these findings with Walker's work on the phylogeny of this insect.*

INTRODUCTION

Over the past few years, Dr. E. M. Walker (1931–1949) of the University of Toronto has published a series of monographs devoted to the anatomy and phylogenetic significance of *Grylloblatta campodeiformis*. In this study there remained the nervous system to be dissected and described. It was, therefore, with the greatest of pleasure that, I, a former student of Dr. Walker's, agreed to carry on his work.

The present work, which is in reality only an introduction to a more complete neurological investigation of this unusual insect is based upon a few alcoholic specimens collected by Dr. Walker at Jasper National Park and three freshly killed individuals obtained through the kindness of Mr. J. D. Gregson of Dominion Veterinary and Medical Entomological Laboratory, Kamloops, B. C. These latter specimens were fixed in alcoholic Bouin's solution, serially sectioned at 10 μ and stained with Heidenhain's iron haematoxylin. Throughout this study frequent references will be made to the brain and nervous system of other orthopteroid insects. These remarks are based upon recent dissection and upon a paper by the author (Nesbitt, 1941).

MORPHOLOGICAL STUDIES OF THE NERVOUS SYSTEM

I. The Supra–oesophageal Ganglion

The brain or more correctly the supra-oesophageal ganglionic mass (Fig. 1, 5) presents few deviations from the plan of the typical orthopteran brain. It is a compact mass which fits down and about the pharynx and rests upon the tentorium; it is held in place by its nervous connectives, by the large muscles of the head and by its own mesenchymal attachments. In keeping with the prognathous nature of the head the supra-oesophageal ganglion (Fig. 1) has been flattened and revolved on its optic axis so that the "true" anterior face of the brain is parallel with the dorsal surface of the head as it is in *Termopsis angusticollis* Hagen. The protocerebral portion of this ganglionic mass produces laterally the slender optic tracts and relatively small optic lobes (LO), dorsally the tegumentary nerves (NT) passing to the occipital region of the head capsule, and posteriorly the occipital nerves (NO) leading to the oesophageal ganglia; the deutocerebral portion, which takes the form of a distinct lobe on each side of the brain, possesses only two pairs of nerves, viz., the large sensory nerves (NA) of the antennae (the olfactory lobes of many authors), and the smaller motor nerves (NAA) to the muscles controlling these appendages. Ventrad and continuous with these ganglionic masses, and on either side of the pharynx, lie the lobes of the tritocerebrum. Each of these continues ventrally as the circumoesophageal commissure (C) leading to the sub-oesophageal ganglion and from each arises a labrofrontal nerve. One branch of this nerve, the pars frontalis (PF) supplies the frontal ganglion (GF); the other branch, the pars labralis (PL) carries the motor and sensory nerves to and from the labrum. Closely associated with the circumoesophageal commissures are the minute tritocerebral commissures (TC).

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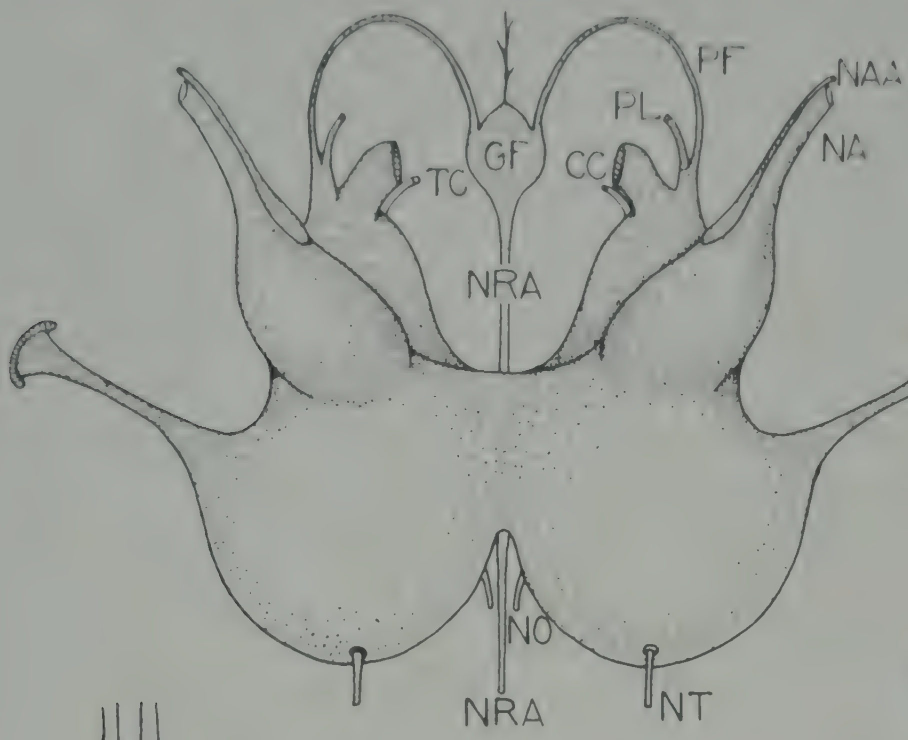
[1] It might be drawn to the attention of readers that when the officers of the Tenth International Congress of Entomology were seeking for a distinctive Canadian insect to act as the symbol or motif of the Congress they chose the creature whose nervous system is herein discussed.

From the preliminary histological studies that have so far been made it appears that the neurological anatomy of the brain of *Grylloblatta* is very similar to that of *Ceuthophalus brevipes* Scudder or *Termopsis angusticollis* Hagen. The cellular cortex, the central complex,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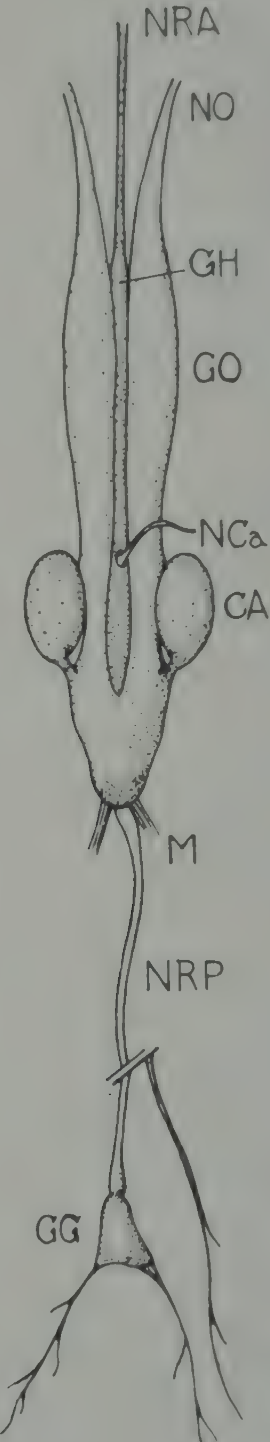
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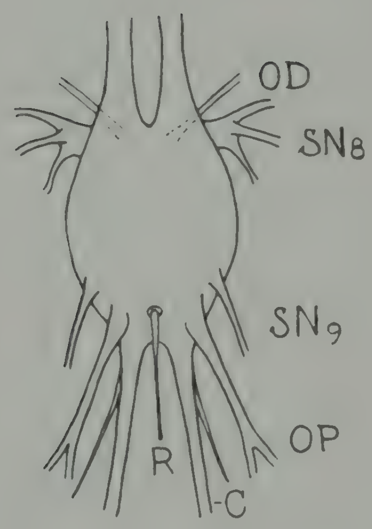
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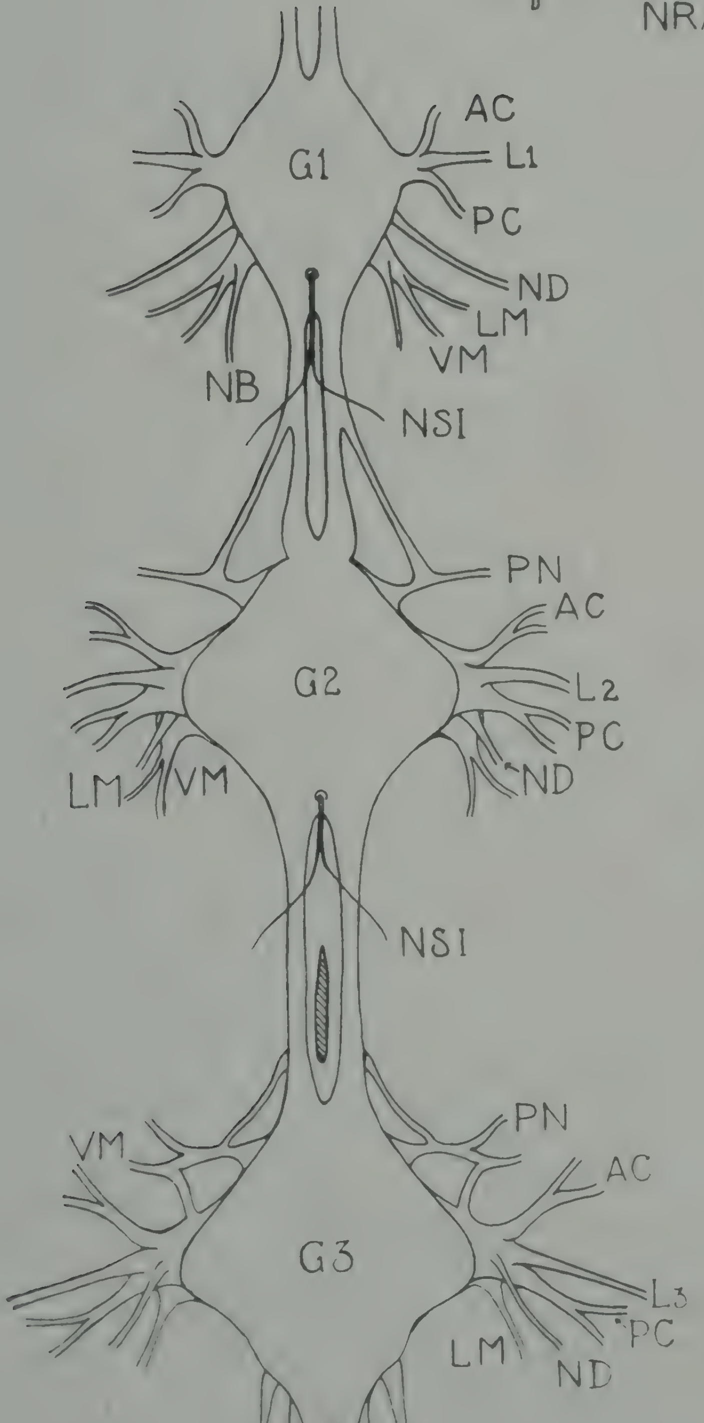
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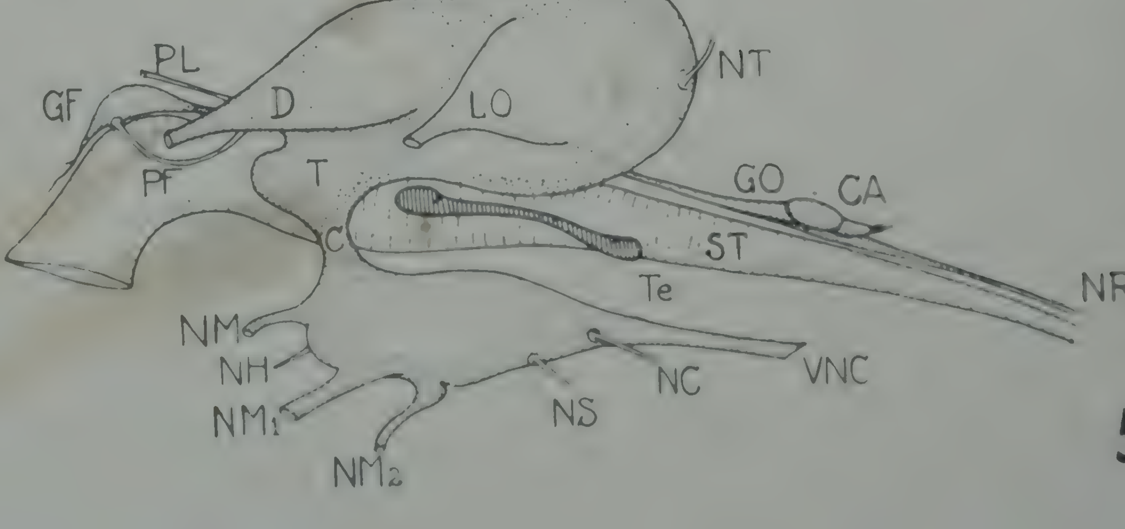
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the corpora pedunculata (mushroom bodies of Thompson, 1913) and the antennal glomeruli are roughly comparable in all three species. The optic lobes, however, are smaller than in *Ceuthophilus* but larger and somewhat more elaborately connected than in *Termopsis*. On comparison with *Mantis religiosa* L., *Dissosteira carolina* (L.), *Blaberus cranifer* Burm. or even *Gryllus assimilis* Fabr. the supra-oesophageal ganglion of the species under discussion seems to be much more primitive in its neurological development. Part of this lack of apparent complexity may be caused by the relatively small development of the optic apparatus and the complete lack of ocelli and their attendant ganglia. The relatively poor development, however, of the corpora pedunculata when compared with these structures in *Mantis* or *Dissosteria* cannot be attributed to these causes alone but might be correlated with the phylogenetic position of these insects or even with their behaviour patterns.

II. The Ventral Ganglionic Chain

(a) The Sub-oesophageal Ganglion

The sub-oesophageal ganglion (Fig. 5) is deeper or thicker than it is wide. On gross examination and on the basis of histological preparations it appears to be composed of the fused ganglia of the mouth-parts. Accordingly, the largest nerves are the paired motor nerves (NM) of the mandibular muscles, the sensory-motor nerves of the maxillae (NM_1) and of the labium (NM_2). In addition to these a single small nerve (NH), which bifurcates shortly after leaving the ganglion, supplies the hypopharynx; a pair of slightly larger nerves (NS) activate the salivary glands; and a second pair of small nerves (NC) supply the neck muscles. As in the case of the brain proper this ganglion stands intermediate in position between that of *Ceuthophilus* and *Termopsis*. It differs from the former in being longer and narrower (in coronal section) and from the latter in being somewhat deeper and in having the circum-oesophageal commissures nearer the anterior end. As the points of origin of the nerves and the internal position of the ganglia are fundamentally similar in all three species these differences would appear to be of little significance.

(b) The Thoracic Ganglia

Because of the nature of the specimens at my disposal, it was well-nigh impossible to follow most of the thoracic nerves to their termination. It was, however, possible to trace them to the large groups of muscles which they supplied. From the prothoracic ganglion (Fig. 4) an anterior group of nerves (AC) supply the tergal promotors (Walker, 1938, muscle no. 60), the anterior rotators (Walker no. 64) the tergosternal muscles (Walker nos. 53 and 54), the pleural promotors (Walker no. 61), the protergal neck muscles (Walker no. 52) and the levator of the trochanter (Walker no. 66); a posterior group (PC) of nerves supply the tergal remotors (Walker no. 62), the adductors of the coxa (Walker no. 65), and the depressor of the fore trochanter (Walker no. 67). The abductor of the fore coxa (Walker no. 63) may be supplied from this group. This statement might be questioned because in none of the specimens dissected was the course of the nerve too clear. Other nerves (L) supply the leg, ND lateral wall and oblique dorsal muscles (Walker no. 56) and (VM) the ventral longitudinal muscles (Walker no. 57). An interesting feature of the thoracic ganglionic chain, and one which is common to all orthopteroid insects is the

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Fig. 1. Dorsal view of the supra-oesophageal ganglion. Fig. 2. Dorsal view of the stomatogastric system. Fig. 3. Dorsal view of the eighth abdominal ganglion. Fig. 4. Dorsal view of the thoracic ganglia. Fig. 5. Lateral view of the supra- and sub-oesophageal ganglia *in situ*.

AC, nerves to anterior group of leg muscles. C, nerves to the cerci. CA, corpora allata. CC, circumoesophageal connectives. CG, brain or supra-oesophageal ganglion. D, deutocerebrum. GI, prothoracic ganglion. GII, mesothoracic ganglion. GIII, metathoracic ganglion. GF, frontal ganglion. GG, gastric ganglion. GH, hypocerebral ganglion. GO, oesophageal ganglion. LI, L2 and L3, Nerves to the fore, middle, and hind legs respectively. LM, nerves of the longitudinal muscles. LO, optic lobe. M, ligaments from fused posterior portion of the oesophageal ganglia. NA, nervus antennalis. NAA, nervus antennalis accessorius. NB, nerves of body wall. NC. nervus cervicalis. NCa, nervus cardiacus. ND, nerves to lateral wall and oblique dorsal muscles. NH, nervus hypopharyngealis. NLF, nervus labro-frontalis. NM, nervus mandibularis. NMI, nervus maxillae. NM2, nervus labii. NO, nervus occipitalis. NOP, nervus opticus. NRA, nervus recurrens anterior. NRP, nervus recurrens posterior. NS, nerve of the salivary ducts. NSI, median or subintestinal nerves. NT, nervus tegumentalis. OD, nerves of internal genital apparatus. OP, nerves of second and third valvulae. P, protocerebrum. PC, nerves to posterior group of leg muscles. PF, pars frontalis. PL, pars labralis. R, nerve of proctodaeum. SN8, nerves of segment eight. SN9, nerves of segment nine. T, tritocerebrum. Te, tentorium. VM, nerve of the ventral muscles.

presence of a loop or plexus between the pro- and meso-, and meso- and metathoracic ganglia. The nerve (PN) which arises from this plexus or anastomosis is flattish in cross-section and runs up the side of the haemocoel to whose epithelium and fat bodies it frequently seems to give off fine rumules. In the winged orthoptera it appears to terminate in the wing base. In *Grylloblatta* it fades away in the tergo-pleural area. Arising from the postero-dorsal face of each of the ganglia, as in *Ceuthophilus*, are to be found the median nerves (NSI) which supply the spiracles. As the nerves of the meso- and metathoracic ganglia are similar to those of the prothoracic ganglion, the reader is referred to figure no. 4 for their arrangement.

(c) The Abdominal Ganglia

The disposition of the members of the abdominal ganglionic chain demonstrates very clearly the primitive position of these ganglia. Unlike all of the other orthopterans studied, with the exception of *Diapheromera*, only one ganglion is fused with the metathoracic and of the remaining seven, five remain in their primitive segments, viz., three, four, five, six, and seven. As Walker (1943) has already shown, the second ganglion lies in segment one; the third at the front of, and projecting slightly over, the intersegmental line between segments two and three; four, five, six and seven each lies in its original segment but successively a little farther back. The seventh ganglion is just in advance of the middle of segment seven. The remaining ganglia of segments eight, nine, and ten are fused into one ganglionic mass (Fig. 3) in segment eight. In the female, this structure supplies nerves to the internal parts of the genital apparatus (OD), the musculature of segment eight (SN8) and the first valvula, the musculature of segment nine (SN9) and the second and third valvulae (OP), the musculature of segment ten and the cerci (C). A small median nerve (R) supplies the musculature of the rectum. As the male dissected was immature it is impossible to say with any degree of certainty what structures the immature nerves would supply in the adults. As in the female, however, nerves SN8 and SN9 supply respectively the musculature of segments eight and nine and nerves C the musculature of segment ten and the cerci. The paired nerves OD appear to ennervate the rudiments of the internal portion of the genital apparatus and the unpaired nerve R supplies the rectum.

III. THE STOMATOGASTRIC OR STOMODAEAL SYSTEM

The stomatogastric or stomodaeal system (Fig. 2) is, like that of all orthopteroid insects, composed of five masses: the precerebral or frontal ganglion (GF) lying on the dorsal face of the stomodaeum and connected to the brain by the pars frontalis (P.F) of the labrofrontal nerve; the hypocerebral ganglion (G.H) which in the insect is little more than an enlargement of the anterior recurrent nerve (NRA) as it passes backward over the stomodaeum posterad of the brain proper; the paired oesophageal ganglia (GO) lying above and intimately fused with the hypocerebral ganglion and joined to the protocerebrum by the occipital nerves (NO); the paired corpora alata (CA) lying laterad of the oesophageal ganglia and joined to them by short connectives; and the single gastric ganglion (GS) on the dorsal surface of the collum of the proventriculus just laterad of the mid-line where proventriculus flexes forward against the crop. In general appearance this system is most similar to that found in the walking-stick *Diapheromera* or the termite *Termopsis*. It differs from both, however, in that the posterior recurrent nerve (NRP) gives rise to a large branch shortly after it emerges from the hypocerebral—oesophageal ganglionic mass. In none of the specimens examined did this nerve give any suggestion of forming a ganglion similar to the gastric ganglion. This insect thus differs quite markedly from *Ceuthophilus*, *Gryllus* and *Dissosteira*, all three of which possess two distinct posterior recurrent nerves each of which terminates in a distinct gastric ganglion. As in the other orthopteroid insects studied a small nerve filament arises from the hypocerebral ganglion to run dorsad to the heart.

CONCLUSIONS

Before we can come to any definite conclusions about the affinities of *Grylloblatta* we have to satisfy ourselves about the amount of emphasis which should be placed upon the facts derived from the nervous system as opposed to those supplied by other related systems within the body. On the bases of his work on the muscular and digestive systems Walker (1949) came to the conclusion that *Grylloblatta* has definite affinities with the Saltatorian suborder Ensifera. On the basis of the inner structure of the proventriculus alone, he believes *Grylloblatta* differs so markedly from any known family of Ensifera that it warrants at least subordinal rank. The findings which I have reported above in the main substantiate this view. The brain itself is similar to that of *Ceuthophilus* but the stomatogastric system and the primitive arrangement of the nerves of the thoracic and abdominal ganglia are sufficiently different from those of the known Ensifera, if not unique, to raise doubts about the close relationship of this insect to any of the other described forms.

REFERENCES

Ander, K. 1939. Vergleichende anatomische und physiologische Studien über die Ensifera. *Opusc. Entomol.* Suppl. 2.

Nesbitt, H. H. J. 1941. A comparative morphological study of the nervous system of the Orthoptera and related orders. *Ann. Ent. Soc. Amer.* 34(1): 51–81.

Thompson, Caroline B. 1913. A comparative study of the brains of three genera of ants, with special reference to the mushroom bodies. *J. Comp. Neurol.* 23(6): 515–572.

Walker, E. M. 1931. On the anatomy of *Grylloblatta campodeiformis* Walker. 1. Exoskeleton and musculature of the head. *Ann. Entomol. Soc. Am.* 24(3): 519–536.

Walker, E. M. 1933. On the anatomy of *Grylloblatta campodeiformis* Walker. 2. Comparisons of head with those of other orthopteroid insects. *Ann. Entomol. Soc. Am.* 26(2): 309–344.

Walker, E. M. 1938. On the anatomy of *Grylloblatta campodeiformis* Walker. 3. Exoskeleton and musculature of neck and thorax. *Ann. Entomol. Soc. Am.* 31(4): 588–640.

Walker, E. M. 1943. On the anatomy of *Grylloblatta campodeiformis* Walker. 4. Exoskeleton and musculature of the abdomen. *Ann. Entomol. Soc. Am.* 36(4): 681–706.

Walker, E. M. 1949. On the anatomy of *Grylloblatta campodeiformis* Walker. 5. The organs of digestion. *Can. Journ. Res., D,* 27: 309–344.

Specialized Areas on the Body Surface of Grasshoppers and Locusts (Orthoptera, Acrididae)

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ABSTRACT

The cuticle of the body wall of an insect and the underlying cells which produce it may exhibit striking modifications in different regions of the individual. In some parts the cuticle furnishes efficient protection from the surrounding environment while in others its chemical and physical properties are such that exchanges of various kinds are possible between the insect and its environment. The cuticular surfaces of a number of species of grasshoppers and locusts have been studied during embryonic and nymphal development and in the adult insect. Regions which are adapted for such purposes as the uptake and retention of water, for adhesion to surfaces and for the penetration of various agents which stimulate sense organs are discussed.

The insect body wall exhibits great diversity in structure and function. It varies in different species in its thickness, rigidity, color, opacity, in its permeability to various materials, in the number of layers of which it is composed and in the substances which they contain. Primarily, of course, it is a skeleton. It protects and supports the soft tissues and serves as a place of attachment for muscles and other organs. But since it serves also as the barrier between the external environment and the interior of the insect it must be modified in certain regions so that specific agents may enter or leave through it at suitable rates or some parts move in relation to others to permit locomotion and other activities. With all of this most entomologists are well-acquainted. It is probable, however, that many are not equally aware of the diversity which may be found in a single individual of a particular group. During the past twenty years much of my own research has been concerned with the cuticular and cellular structures which form the body surfaces of grasshoppers and locusts. The species most intensively studied have been *Melanoplus differentialis differentialis* (Thomas), *Melanoplus mexicanus mexicanus* (Saussure), *Romalea microptera* (Beauvois) and *Locusta migratoria migratorioides* (Reiche and Fairmaire). Several hundred other species have been studied in a more superficial way. This paper is an attempt to bring together some of the results of these investigations. Since much must be omitted attention will be focussed, for the most part, on only a few of the properties of the body wall and foremost among these will be its ability to permit or prevent the passage through it of water and other agents.

The greater part of the body wall of a grasshopper or locust resembles quite closely the diagrams seen in textbooks and reviews (Snodgrass, 1935; Wigglesworth, 1948, 1950; Weber, 1949; Richards, 1951) and which represent a section through the integument of a typical insect. It consists of a layer of epidermal cells which is bounded internally by a thin basement membrane and externally by a cuticle which is composed of several layers. The epidermal cells may be columnar, cuboidal or flattened. They may lie in a single layer or else be crowded together so that they no longer appear as a single layer. Beneath them lies a basement membrane which is not conspicuous in slides made with the commoner histological techniques but which in suitable silver preparations (Slifer, 1952) or, occasionally, in those made with methylene blue is seen to consist of an intricate and beautiful web of extremely fine fibers. The cuticle, which is produced by the epidermis and covers it externally, consists of the usual three layers—epicuticle, exocuticle and endocuticle. The first of these, although very thin, is highly impermeable to water and this impermeability is little affected when lipoid solvents are applied to it externally for brief periods and at moderate temperatures. Thus the epicuticle forms an efficient barrier to the loss or uptake of water and to many substances dissolved in water. The exocuticle is sclerotized and is responsible for the rigidity of the body wall while the endocuticle, in contrast, is tough and flexible. Variations in the absolute and relative thickness of the exocuticle and endocuticle account largely for the differences in the rigidity or flexibility of different parts of the body wall. The exocuticle and endocuticle together provide protection from mechanical injury while the epicuticle minimizes possible damage from excessive loss or uptake of water and other chemicals. Large numbers of fine pore canals pass upwards through the cuticle and stop just short of the outer surface. Here and there larger canals penetrate the cuticle and open on its surface. These are the ducts of the epidermal glands and each arises in the epidermal layer inside a single gland cell. Briefly, these are the most striking features of the greater part of the body wall of a grasshopper or locust. The remainder of this paper will be concerned with certain specialized regions where the body wall differs in some way from that just described.

One of the first of the cuticular membranes which I studied was that which is formed just inside the inner surface of the chorion of the grasshopper egg during its development (Slifer, 1937). A few days after the egg is laid this membrane is secreted by the serosal cells which, at this time, form a continuous layer over the yolk. In every important respect this cuticle so closely resembles that of an adult insect that there is good reason for thinking of it, together with the serosal cells which produce it, as the first body wall of the new individual. The embryonic cuticle consists of two distinct layers the outermost of which is thin, yellow in color, highly impermeable to water and very resistant to injurious chemicals while the innermost is thick, white, laminated, flexible, tough and porous, and is penetrated by many fine pore canals. Chitin is absent in the outer layer but present in the inner. Like the epicuticle of the adult the permeability of the outer layer is little affected by wax solvents. The serosa, which secretes the embryonic cuticle, might well be considered the first epidermal layer although it does lack a basement membrane—or, more accurately, none has yet been demonstrated—and so differs from the definitive epidermis of the adult. Shortly before hatching is due the tough inner layer of the embryonic cuticle is digested away by a secretion produced by special embryonic glands—the pleuropodia. The digestion of the inner cuticular layer is strikingly similar to the digestion of the inner layers of the cuticle of the nymphal body wall just before each molt. One region of this embryonic cuticle differs from the rest. In a small, circular patch at the posterior end of the egg both the cuticle and the cells below it are modified. Here the outer layer is much thicker and the inner much thinner than elsewhere. The large serosal cells associated with this region are columnar in shape instead of being flattened. When first formed this specialized, cuticular patch or hydropyle, as I have called it (Slifer, 1938), is readily permeable to water. Just before diapause begins a delicate layer of wax is secreted onto the surface of the hydropyle by the cells which lie below it. This prevents uptake of the additional water required by the egg for further development. Towards the end of diapause the hydropyle again becomes permeable, water is absorbed and the egg resumes development. If, during diapause, the egg is treated with a wax solvent the wax layer which covers the hydropyle is dissolved away, water now passes in through the hydropyle and development begins once more (Slifer, 1946, 1948, 1949a, 1949b, 1950b).

Turning now to the adult or nymph we find that there are certain specialized parts of the body wall which resemble the hydropyle of the egg during diapause in that, although normally impermeable to water, treatment with wax solvents removes the protective wax covering on the surface. The underside of the tarsus and of the arolium are among these (Slifer, 1950a). Species of Acrididae which belong to certain subfamilies, such as the Cyrtacanthacridinae, are able to climb smooth surfaces. In such species the arolium is large and its underside is covered with a thick, soft cuticle so smooth and glossy that it adheres closely to the surface against which it is placed. In sectioned material the widest of the layers of this cuticle is seen to be composed of many soft, rod-like structures which lie parallel to one another and extend at right angles from the surface. These are attached to one another by many delicate strands. At its outer end each rod divides into a brush-like tuft of smaller rods. Perhaps these rods arise from pore canals which later become filled with cuticular material, as has been reported for a number of insects and crustacea (Richards, 1951). Between the layer of rods and the epidermal cells lies a loose layer of irregularly-arranged cuticular fibers. The epidermal cells are unusual in that tufts of these fibers extend up into them so that individual cells seem to be impaled on them. The soft pads or euplantulae which are on the underside of the tarsus possess a cuticle which is intermediate between that of the arolium and that of the general body surface. The surface here is also extremely smooth but it differs from that of the arolium in that wax solvents have little effect on it. Oddly, the proximal pair of metathoracic euplantulae differs from the others in that its waterproof covering does dissolve readily in wax solvents.

Other curious structures present on the body surface of grasshoppers and locusts are the antennal crescents and fenestrae (Slifer, 1951). These are paired, segmentallyarranged regions, of characteristic and often extraordinary shapes. Here the cuticle is thin, soft and contains pore canals which are filled with air. The surface of the cuticle is extremely smooth and the waxes present on it are easily removed with xylol. The epidermal cells which lie beneath this specialized cuticle are unusual in that they are provided at their inner ends with a number of conspicuous, finger-like projections which extend laterally and fit in between those of neighboring cells. Experimental evidence suggests that these specialized regions are more sensitive to heat than are adjacent parts of the body wall and that they may serve as thermoreceptors of a primitive sort. However it is not certain that this is their sole or even their most important function.

The regions of the body surface so far considered have all been covered with materials which, under normal conditions, are highly impermeable to water, although one of these —the hydropyle of the egg—does permit water to pass through it when the egg is not in diapause. It was particularly interesting, then, to find a few years ago that there are parts of the body wall of the grasshopper nymph and adult which are freely permeable to water. These are the tips of certain of the sensory pegs (Slifer, 1954a, 1954b, 1955a, 1955b). Three types of basiconic sensilla are present on the antennal flagellum and of these the longest has a cuticle which is not especially unusual except at its tip and here, in an area which is only a few microns in diameter, waterproofing materials are absent. It may even be possible that none of the usual layers of the cuticle are present here. However, in fresh preparations which are examined under an oil immersion lens a very delicate membrane can be seen covering the tip. Whatever the origin or composition of this membrane water and dyes in aqueous solution pass through it readily and there is no need to treat the surface first with a wax solvent. These long, permeable basiconic pegs are present not only on the antennal flagellum but on most of the other parts of the body surface as well and experimental evidence has been obtained which indicates that they are sensitive to highly-concentrated, repellent odors. Another type of sense organ, the coeloconic peg, is also present on the antennal flagellum but is not known to occur elsewhere on the body. Experiments suggest that these may be the sense organs which enable the grasshopper to find water for they also have permeable tips and grasshoppers which have had the flagella of their antennae removed are no longer able to detect water vapor. At the moment, however, it is not possible to rule out the two smaller types of basiconic pegs as hydroreceptors for they, too, seem to be restricted to the antennae. Quite recently these two types have been found to possess very minute spots, near the base, which can be colored when a dye in aqueous solution is applied to the outer surface of the antenna of the living insect.

Perhaps you have noticed that there is a common thread which runs through all of the studies summarized here. In each such questions as the following have been raised: Does water or some other agent pass through this particular part of the body wall in significant amounts under natural conditions? How resistant is the surface to alteration by chemical or physical means? Does the cuticle or the epidermis show any distinctive structure when examined under the microscope? With the answers to such questions as a starting point investigations have been pursued in various directions in an attempt to discover or clarify the functions of those regions which are in some way different from the rest.

REFERENCES

Richards, A. G. 1951. The integument of arthropods. *Univ. of Minnesota Press*, Minneapolis.

Slifer, E. H. 1937. The origin and fate of the membranes surrounding the grasshopper egg; together with some experiments on the source of the hatching enzyme. *Quart. Jour. Micro. Sci.* 79: 493–506.

Slifer, E. H. 1938. The formation and structure of a special water-absorbing area in the membranes covering the grasshopper egg. *Quart. Jour. Micro. Sci.* 80: 437–457.

Slifer, E. H. 1946. The effects of xylol and other solvents on diapause in the grasshopper egg; together with a possible explanation for the action of these agents. *Jour. Exp. Zool.* 102: 333–356.

Slifer, E. H. 1948. Isolation of a wax-like material from the shell of the grasshopper egg. *Discuss. Faraday Soc.* 3: 182–187.

Slifer, E. H. 1949a. Changes in certain of the grasshopper egg membranes during development as indicated by fast green and other dyes. *Jour. Exp. Zool.* 110: 183–203.

Slifer, E. H. 1949b. Variations, during development, in the resistance of the grasshopper egg to a toxic substance. *Ann. Entom. Soc. Amer.* 42: 134–140.

Slifer, E. H. 1950a. Vulnerable areas on the surface of the tarsus and pretarsus of the grasshopper (Acrididae, Orthoptera); with special reference to the arolium. *Ann. Entom. Soc. Amer.* 43: 173–188.

Slifer, E. H. 1950b. A microscopical study of the hydropyle and hydropyle cells in the developing egg of the grasshopper, *Melanoplus differentialis. Jour. Morph.* 87: 239–273.

Slifer, E. H. 1951. Some unusual structures in *Locusta migratoria migratorioides* and their possible function as thermoreceptors. *Proc. Roy. Soc., B*, 138: 414–437.

Slifer, E. H. 1952. Connective tissue in the locust. *Anat. Rec.* 113: 572 (abstract).

Slifer, E. H. 1954a. The permeability of the sensory pegs on the antennae of the grasshopper (Orthoptera, Acrididae). *Biol. Bull.* 106: 122–128.

Slifer, E. H. 1954b. The reaction of a grasshopper to an odorous material held near one of its feet (Orthoptera: Acrididae). *Proc. Roy. Entom. Soc. London* 29: 177–179.

Slifer, E. H. 1955a. The distribution of permeable sensory pegs on the body of the grasshopper (Orthoptera: Acrididae). *Entom. News* 66: 1–5.

Slifer, E. H. 1955b. The detection of odors and water vapor by grasshoppers (Orthoptera, Acrididae) and some new evidence concerning the sense organs which may be involved. *Jour. Exp. Zool.* 130: 301–318.

Slifer, E. H. 1956. The response of a grasshopper, *Romalea microptera* (Beauvois), to strong odours following amputation of the metathoracic leg at different levels. *Proc. Roy. Entom. Soc. London* 31: 95–98.

Snodgrass, R. E. Principles of insect morphology. *McGraw-Hill*, New York.

Weber, H. 1949. Grundriss der Insektenkunde. *Fischer*, Jena.

Wigglesworth, V. B. 1948. The insect cuticle. *Biol. Rev.* 23: 408–451.

Wigglesworth, V. B. 1950. The principles of insect physiology. *Methuen and Co.*, London, 4th edition.

DISCUSSION

P. J. H. CHRISTENSEN. Have you not had difficulties in sectioning the yolk?

E. H. SLIFER (MISS). Yolky eggs and many other materials which are difficult or impossible to section in paraffin with ordinary techniques can be cut easily if the tissue is exposed to water after it is embedded in paraffin. Details of the method may be found in a paper published in Science by Slifer and King in 1933 (vol. 78, p. 366).

F. H. BUTT. Does the embryonic cuticle form on the embryo only? What is its relation to the amnion and serosa?

E. H. SLIFER (MISS). The serosa, when first formed, lies just below the chorion. It is a continuous cellular layer which encloses all of the egg contents. Soon after its formation the serosa begins to secrete the first embryonic cuticle from its outer surface and this new layer then separates the chorion from the serosa. The amnion, at this time, covers the ventral surface of the embryo only. It is not in contact with the cuticle and plays no part in its formation. Later, a *second* and then a *third* cuticle are secreted by the epidermal cells of the embryo's body wall. These cuticles are shed as soon as the young grasshopper leaves the egg while the remnants of the first cuticle are left attached to the inner surface of the chorion. The cuticle of the body wall of the first instar nymph is actually the *fourth* cuticle formed and is secreted shortly before hatching occurs.

J. P. DAVEY. Could Dr. Slifer please say a little more about coeloconic receptors, and her laboratory experiments which lead her to believe that grasshoppers can detect the presence of moisture by these organs? Also, could she enlarge upon Dr. Spencer's view that in the field grasshoppers can detect moisture over a considerable distance?

E. H. SLIFER (MISS). Normal grasshoppers which have been deprived of food and water for 24 hours will start moving towards a dish of water very soon after it is placed in their cage while grasshoppers which have had their antennal flagella removed show no such response. Of four types of sensory pegs found on the antenna three types—one coeloconic and two different kinds of short basiconic peg—are found nowhere else on the body. Until very recently the evidence on hand indicated that the coeloconic peg was probably the receptor which was sensitive to water vapor. However, within the past few weeks new evidence has been obtained which hints that the short basiconic pegs can not be ruled out as possible hydroreceptors.

Dr. G. J. Spencer kindly permitted me to see some of his records taken in the field in which he had noted that *Melanoplus mexicanus* may respond positively to water from a distance as great as 70 feet.

Calcium Oxalate Crystals in the Cuticle of Certain Insect Larvae

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ABSTRACT

The cuticle of Anisota senatoria (*Lepidoptera*) *larvae comprises a tanned epicuticle, an untanned exocuticle (mesocuticle), and a thick endocuticle. Immediately beneath the epicuticle, embedded in the exocuticle, is found a layer of short prismatic crystals of calcium oxalate. These crystals appear just before ecdysis during the deposition of the cuticle. They are shed with the exuviae at each molt.*

The crystals are present in the soft cuticle of all larval instars of Anisota senatoria, *but are absent from the heavily tanned areas such as the head, prolegs, spines, and muscle insertions. They are also absent from the cuticular linings of the fore-gut, hind-gut and tracheae. No crystals are found in the cuticle of pupae or adults.*

A survey of 147 species of immature insects in 11 orders revealed 13 species (12 Lepidoptera, 1 Hymenoptera) with calcium oxalate crystals in the cuticle. The lepidoterous larvae with crystals are in the families Citheroniidae (Anisota senatoria, A. stigma, A. virginiensis, A. consularis, A. rubicunda), *Sphingidae* (Ceratomia catalpae, C. amyntor, Phlegethontius sexta, P. quinquemaculatus, Sphinx chersis, Smerinthus *sp.*), *and Nymphalidae* (Polygonia interrogationis). *The single hymenopteran with cuticular crystals is* Fenusa pusilla.

The maximum crystal length ranges from 2-20 microns. The crystals are all prismatic, but vary from nearly cubical forms to long narrow prisms. They may be scattered throughout the cuticle (Sphinx chersis), *but in most species are found embedded near the surface. The size, shape, and location of the crystals are constant for a particular species.*

INTRODUCTION

Calcium oxalate crystals are commonly found in the Malpighian tubules of many insects (Wigglesworth, 1950). Deposits of calcium oxalate have also been reported in the oöthecae of roaches (Hallez, 1909) and the egg shells of phasmids (Pantel, 1919). Large amounts of calcium carbonate are deposited in the cuticle of the last larval instar of the cherry fly, *Rhagoletis cerasi* (Wiesmann, 1938), but there appear to have been no reports of the occurrence of calcium oxalate in the cuticle of insects. It was therefore of considerable interest to find a layer of calcium oxalate crystals just beneath the surface of the larval cuticle of *Anisota senatoria* (A. & S.), the orange-striped oak-worm (Lepidoptera, Citheroniidae).

IDENTIFICATION OF CRYSTALS IN CUTICLE OF *ANISOTA*

In sections of the fifth instar larval cuticle stained with Mallory's triple stain, the crystals appear as a row of colorless, cuboidal structures embedded in the red-staining exocuticle just below the surface (Fig. 4, crys). When these structures were examined with polarized light they were found to be highly birefringent, thus strongly indicating a crystalline nature. Ashing of the cuticle demonstrated that they were inorganic crystals, since ash remained only in those portions of the cuticle containing the crystals. The crystals are insoluble in water and acetic acid, but are readily soluble in mineral acids and potassium hydroxide. The shape and solubilities of the crystals suggested that they were calcium oxalate. They are also insoluble in concentrated sodium hypochlorite, a test Ito (1924) used for calcium oxalate in roach oöthecae. Chemical and histochemical tests for the calcium and oxalate ions were performed to definitely establish the identity of the crystals.

The crystals in sections stained bright orange with alizarin red S. Ashed cuticle treated with 1% sulfuric acid showed rapid formation of rosettes of needle-shaped gypsum crystals. If a hydrochloric acid solution of the ash was neutralized and dilute ammonium oxalate was added, a copious white precipitate of calcium oxalate appeared. A platinum wire flame test was also positive for calcium. These tests clearly established the presence of the calcium ion.

Confirmation of the presence of oxalate was more difficult since the organic materials in the cuticle interfere with the tests commonly used, and the oxalate ion is destroyed by ashing. Therefore the crystals were extracted from the cuticle with hydrochloric acid and reprecipitated by neutralization with ammonium hydroxide before oxalate tests were conducted. Feigl (1943) described a specific test for oxalate based on the formation of aniline blue when diphenylamine and oxalic acid react. A very strong positive reaction was obtained when this test was applied to the precipitate obtained from the cuticle extract. Oxalates decolorize potassium permanganate in acid solutions. If some of the precipitate was dissolved in 1 N sulfuric acid and drops of 0.05 N potassium permanganate were added, they were quickly decolorized. This confirmed the presence of the oxalate ion in the precipitate.

OCCURRENCE OF CALCIUM OXALATE CRYSTALS IN DEVELOPMENTAL STAGES OF *ANISOTA SENATORIA*

The eggs, larvae, pupae, and adults of *Anisota senatoria* were examined to determine the distribution of the calcium oxalate crystals. When the chorion of the eggs is viewed with polarized light, birefringent fibers are apparent but no crystals are seen. Crystals are not found in the vitelline membrane, but peculiar dumbbell-shaped crystals are present in the yolk just beneath the membrane. These are also found in the yolk inside the embryonic gut and are still present in the gut of newly-hatched larvae. Their solubilities indicate they are probably calcium oxalate crystals.

All five larval instars of *Anisota* have a layer of calcium oxalate just beneath the epicuticle. The crystals are present in the cuticle of the first instar when it hatches from the egg. At each molt they are shed with the exuviae. The average size of the crystals in the exuviae of the last three instars is about the same (2 x 2.5 microns in surface view), but in the first two instars they are slightly smaller (1.4 x 1.7 microns).

The crystal layer is found all over the body cuticle except for regions where tanning of the exocuticle has occurred. The cuticle of the head, thoracic legs, tips of the prolegs, spines, sensillae, spiracles, and muscle insertions contains no crystals. When whole mounts of the cuticle are examined with polarized light, the tanned areas appear as dark holes in the brilliant crystal layer. Ashed exuviae retain their original shape, but the positions of spines and muscle insertions are marked by holes in the ash. Only in parts of the cuticle containing crystals is enough ash present to preserve the cuticular outline.

The ecdysial membrane, the linings of the fore-gut and mid-gut, and the lining of the tracheae do not contain crystals. The principal crystalline material in the Malpighian tubules of *Anisota* larvae is calcium oxalate. In the cuticle of the pupa and adult, which is heavily tanned, no calcium oxalate crystals are found.

THE INTEGUMENT OF FIFTH INSTAR *ANISOTA SENATORIA* LARVAE

The integument of the fifth instar *Anisota* larva comprises the epidermis and the cuticle which the epidermis and certain other cells secrete. The cuticle consists of a thin outer layer, the epicuticle, and a thick inner layer, the procuticle. The procuticle is modified into an exocuticle (Fig. 4, exo) and an endocuticle (Fig. 4, endo). Immediately beneath the epicuticle, embedded in the exocuticle, is found the layer of short prismatic calcium oxalate crystals (Fig. 4, crys). The cuticle is raised into tubercles (Fig. 4, tub) which correspond to the epidermal cells, one tubercle per cell.

Fig. 1. *Anisota senatoria* fourth instar larval cuticle, 3 days after the third molt.

Fig. 2. *Anisota senatoria* fourth instar larval cuticle, 4 1/4 days after the third molt.

Fig. 3. *Anisota senatoria* fourth instar larval cuticle, 5 1/8 days after the third molt (about 3 hours before the fourth molt).

Fig. 4. *Anisota senatoria* fifth instar larval cuticle, 7 days after the fourth molt.

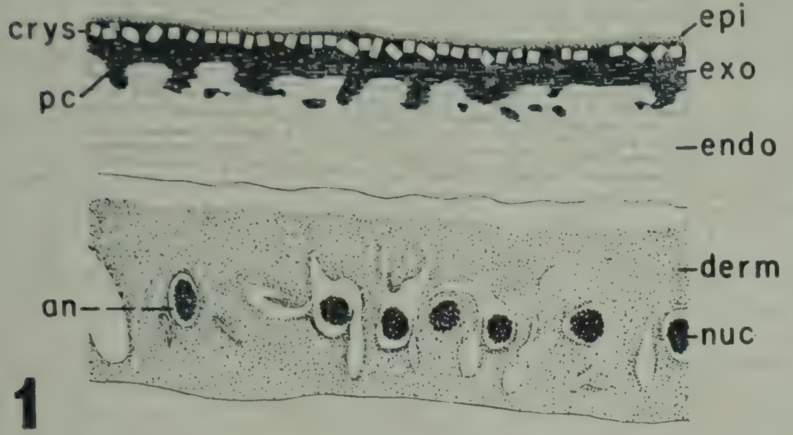
Fig. 5. *Ceratomia catalpae* fifth instar larval cuticle.

Fig. 6. *Sphinx chersis* larval cuticle.

Fig. 7. *Fenusa pusilla* last instar larval cuticle.

Magnification about 450 x. Abbreviations: an, annular space; crys, crystals; derm, epidermis; ecm, ecdysial membrane; endo, endocuticle; epi, epicuticle; exo, exocuticle; exsp, exuvial space; exuv, exuvium; nuc, nucleus; pc, pore canals; pro, procuticle; tan, tanned epicuticle; tub, tubercle; vac, vacuole.

The epicuticle is 2-3 microns thick (Fig. 4, epi). It is pale yellow and does not stain indicating it is probably partially tanned. It also gives a positive argentaffin reaction. When the chitosan-iodine test for chitin (Campbell, 1929) is applied to *Anisota* cuticle, the cuticle outside the crystal layer dissolves demonstrating this part of the cuticle is the nonchitinous epicuticle. The crystals dissolve but the cuboidal spaces in the cuticle can readily be seen. The exocuticle extends between the crystals and in a thin layer over the surface of the crystals in certain regions of the cuticle.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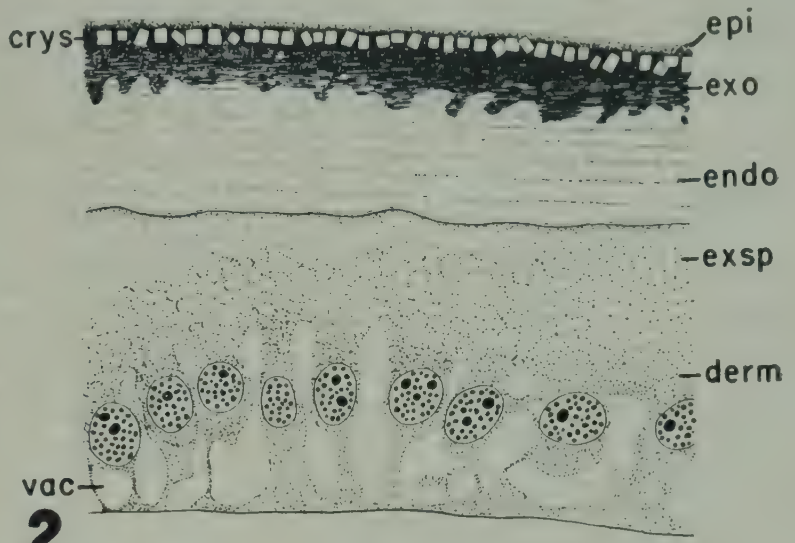
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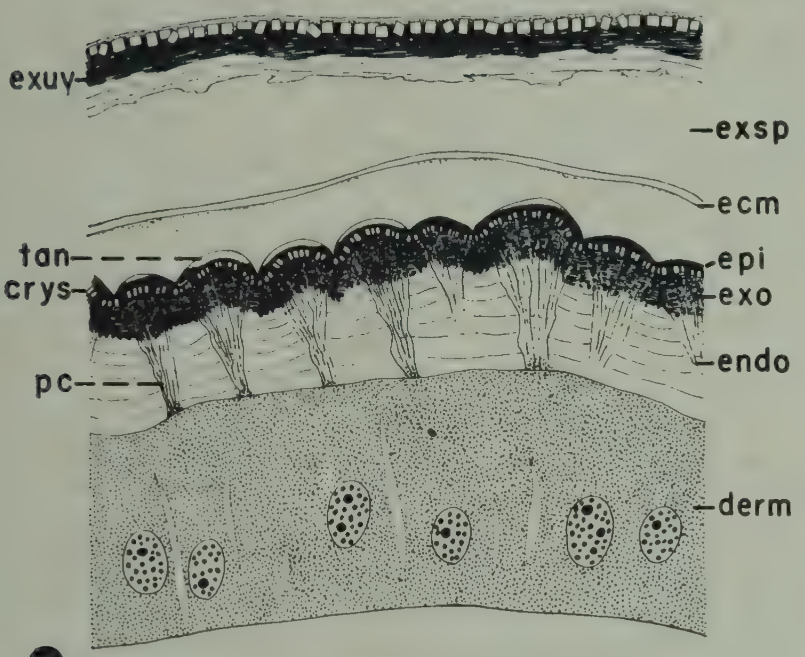
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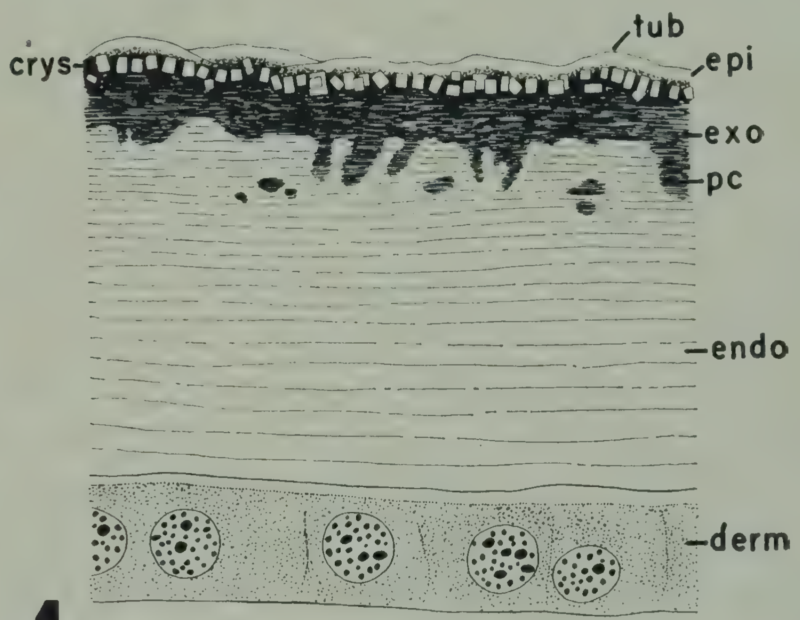
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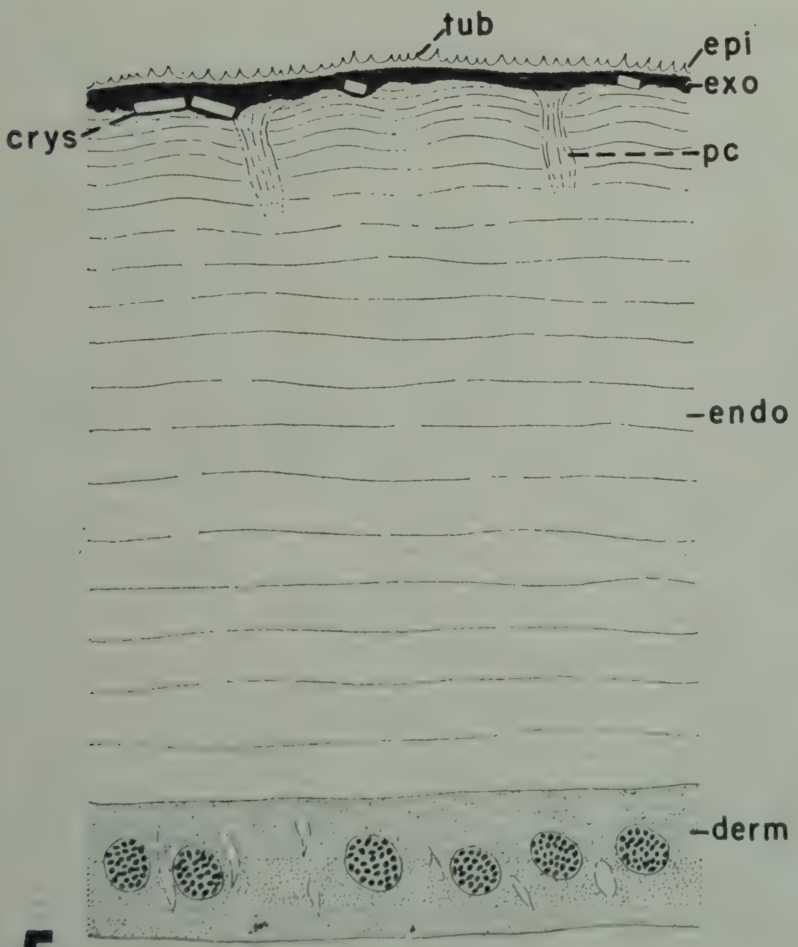
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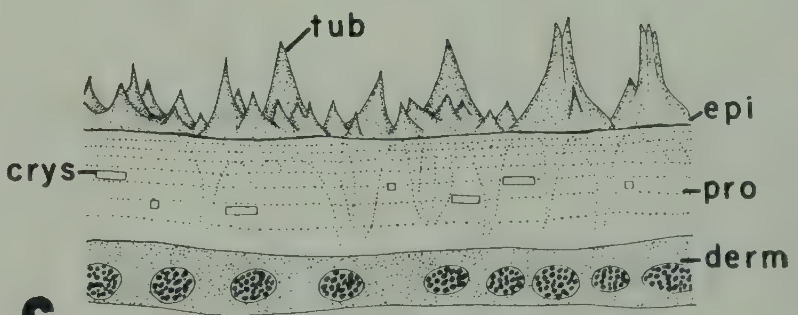
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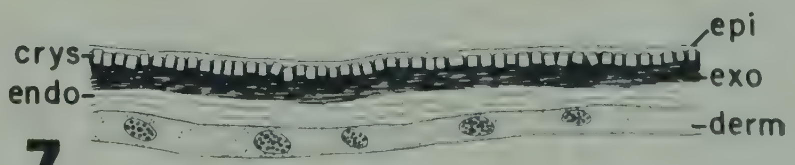
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The procuticle is about 70 microns thick in the late fifth instar larva. When stained with Mallory's triple stain it is seen to be differentiated into an outer red-staining exocuticle (Fig. 4, exo) and an inner blue-staining endocuticle (Fig. 4, endo). The exocuticle has a very irregular inner boundary and extends between the crystals to meet the epicuticle at the outer surface. Wedges of red-staining material extending into the endocuticle are the remnants of groups of pore canals (Fig. 4, pc).

The cuticle of spines and that at muscle insertions shows tanning of the outer portion of the exocuticle as indicated by a pale yellow to amber color and lack of staining. In these regions there is thus an inner exocuticle and an outer one. It is possible that an extremely thin tanned exocuticle is present over much of the body surface. It would be located just beneath the epicuticle next to the crystals. In some regions tanning has been noted to extend well below the crystals, but this is very spotty in its occurrence.

The cuticle of the four earlier instars does not show the conspicuous tubercles seen in the fifth instar. The epicuticle, which is considerably thinner than in the fifth instar, stains red with Mallory's triple stain and black with iron hematoxylin. It is untanned in the first three instars, but rather pale staining in the fourth instar indicates that a slight tanning may occur.

FORMATION OF FIFTH INSTAR *ANISOTA* CUTICLE

The changes in the integument during the fourth larval molt were followed to study the formation of the calcium oxalate crystals. It was essential to have fourth instar larvae whose exact age, as measured with reference to the third molt, was known. These were isolated in Mason jars with oak leaves for food. After various periods of time they were removed and fixed in Bouin's or Carnoy's fluids. When a complete series of larvae of known ages was assembled, sections were made and stained with Mallory's triple stain and various other stains to follow the details of the formation of the fifth instar cuticle. Since the rate of development of individual larvae varied a great deal, it must be kept in mind that the time given for a particular event is only a close approximation.

Twelve hours after the third molt the fourth instar larvae are actively feeding. The cuticle is 13 microns thick. The pore canals stain red with Mallory's stain and are attached by protoplasmic strands to the epidermis. The epidermis is 20 microns thick with no apparent vacuolation. The nuclei average 6.8 microns in length. The chromatin is evenly distributed in granular form and the nucleoli are readily seen. The crystals average less than a micron on a side.

By three days after the third molt the larvae are feeding less actively. They stop feeding 3 1/2 days after the third molt. The cuticle is now 27 microns thick (Fig. 1), having approximately doubled in thickness. The epidermis is somewhat thicker (30 microns) and vacuoles are seen in the cytoplasm. The nuclei have become pycnotic and appear to pull away from the cytoplasm leaving an annular space (Fig. 1, an). They are 6.3 microns in diameter. The nucleoli are not seen because of the density of the nuclei. The crystals have increased in size to about two microns on a side and also appear to be more numerous. They change little in size from this stage until the cuticle is shed at the end of the fourth molt.

The cuticle remains essentially unchanged at 4 1/4 days after the third molt (Fig. 2). The epidermis (Fig. 2, derm), however, has become thicker (45 microns), has been thrown into folds, and has pulled away from the cuticle. The cells are very attenuated at their bases with large spaces between them, and the outer part of the cytoplasm is vacuolar in appearance. The nuclei have increased in size to 10.5 microns. Nucleoli are clearly visible and the chromatin in evenly distributed. No mitoses have been observed in the epidermis, although they are frequently seen in the fat body cells at this time.

Four and three-eighths days after the third molt the larvae are stationary on the leaves and very turgid in appearance. The digestion of the fourth instar cuticle has begun and the ecdysial membrane is clearly visible as a dark blue-staining layer (with Mallory's stain) at the inner surface of the endocuticle. At this time the new fifth instar cuticle is first seen. It already consists of the epicuticle and about 10 microns of the procuticle. The secretion of these layers must be very rapid since three hours previously there was no indication of them. The epicuticle stains bright red, the procuticle blue. The pore canals are seen as vertical lines through the procuticle. In this stage the larvae are very pale in color since no pigment is found yet in the new cuticle. The epidermis has changed little in thickness, but it is no longer thrown into folds and the clefts between cells are not seen. Large vacuoles are found in the outer zone of the cytoplasm instead of the fine vacuolation seen three hours earlier. The nuclei are slightly larger with an average length of 11.3 microns, and they remain about this size until the end of the fifth instar.

At 5 1/8 days after the third molt the larvae are dark in appearance because the pigment in the new cuticle is visible through the almost transparent old cuticle. The old cuticle has been digested almost to the exuvial thickness (10 microns). Ecdysis occurs at 5 1/4 days after the third molt. The exuvium (Fig. 3, exuv) consists of the epicuticle, the crystal layer, and 5–8 microns of undigested procuticle. The ecdysial membrane (Fig. 3, ecm) is conspicuous in the space between the exuvium and the new cuticle. The new fifth instar cuticle is about 25 microns thick. The red-staining exocuticular material has accumulated in the outer half of the procuticle almost to the thickness it will finally attain. The pore canals (Fig. 3, pc) are arranged in groups, one per epidermal cell. Tanning of the epicuticle has already begun at the tips of the tubercles (Fig. 3, tan) as indicated by a pale yellow color and lack of affinity for stains. The crystals are first seen in the new cuticle at this time (3–6 hours before ecdysis). They measure less than one micron on a side and are sparsely scattered. They form either in or between the pore canal tips just beneath the epicuticle. The crystals around muscle insertions are larger than those over the rest of the body cuticle since they appear earlier near these heavily tanned areas.

By eighteen hours after ecdysis the larva is feeding actively again. The cuticle has increased slightly in thickness and tanning of the epicuticle is almost complete. The pore canals are marked by red-staining segments extending from the exocuticle down into the endocuticle. The epidermis shows little change. The crystals are now up to 1.5 microns in length. They appear to be more numerous, but this may be partly a result of their increased size.

At about 7 days after the fourth molt the fifth instar cuticle is fully developed (Fig. 4). The tubercles have become flattened out by the stretching of the cuticle as a result of larval growth. The cuticle is 70 microns thick. The epidermis is much thinner (18–20 microns) than it was at 18 hours after ecdysis. The nuclei remain about 11 microns in length, but their longest axis is usually oriented parallel to the cuticle surface rather than perpendicular to it as in previous stages. This change in nuclear orientation may be a result of thinning of the epidermis. The crystals have a maximum length of 2–4 microns. Most are about 2 x 2.5 microns when viewed from the surface of the cuticle. They reach this size by three to four days after ecdysis.

We thus see that the molting processes of the fourth molt in *Anisota* larvae occur during the non-feeding period which begins 42 hours before ecdysis. The marked pycnosis of the epidermal nuclei at this time signals the beginning of the molt. This is followed by a rapid growth of the epidermal cells resulting in a pronounced folding of the epidermis by 24 hours before ecdysis. At this time the epidermis pulls away from the cuticle, the nuclei almost double in length, and digestion of the old cuticle and secretion of the new cuticle begin. Three to six hours before ecdysis the red-staining exocuticular material begins to accumulate in the outer half of the procuticle, pigment is deposited in the epicuticle, tanning starts at the tips of the tubercles, and the calcium oxalate crystals first appear. During the first 24 hours after ecdysis the exocuticle attains its maximum thickness, tanning of the epicuticle is completed, and the crystals more than double in length. From this time until the prepupal stage the cuticle approximately doubles in thickness, and the crystals gradually attain their full size.

It is clear that the calcium oxalate crystals appear and grow most rapidly during the period of maximum activity of the epidermal cells. The crystals are then shed with the exuviae at each molt. There seems little doubt that this is an excretory process. Calcium salts are also excreted by the Malpighian tubules. Preliminary studies to determine the role of exuvial excretion in the total calcium excretion of *Anisota* larvae indicate that a significant percentage of the calcium excreted from the body is removed as calcium oxalate in the exuviae.

CALCIUM OXALATE CRYSTALS IN CUTICLE OF OTHER INSECT LARVAE

A survey of representative immature insects in the orders Ephemeroptera, Odonata, Plecoptera, Hemiptera, Homoptera, Coleoptera, Neuroptera, Hymenoptera, Diptera, Trichoptera, and Lepidoptera was conducted. One hundred and forty-seven species in seventy families were examined to ascertain whether calcium oxalate crystals were present in the cuticle. Crystals were found in the cuticles of thirteen species, twelve in the order Lepidoptera and one in the order Hymenoptera.

In the lepidopterous family Citheroniidae seven species were examined. The caterpillars of *Eacles imperialis* and *Citheronia regalis* have no crystals in the cuticle, but five species in the genus *Anisota* (*Anisota senatoria*, *A. stigma*, *A. virginiensis*, *A. consularis*, and *A. rubicunda*) do have them. The size, shape, and distribution of the crystals in all five species of *Anisota* are very similar.

The caterpillars of the family Sphingidae are of particular interest because of the variability in size, shape, and distribution of the calcium oxalate crystals. *Ceratomia catalpae*, *C. amyntor*, *Phlegethontius sexta*, *P. quinquemaculatus*, *Sphinx chersis*, and *Smerinthus* sp. all have crystals in the larval cuticle. *Hemaris diffinis*, *Pholus achemon*, *P. satellitia*, and *Celerio lineata* have no crystals.

The larval cuticle of *Ceratomia catalpae* (Fig. 5) consists of a thin epicuticle, a thin untanned exocuticle, and a very thick endocuticle. The calcium oxalate crystals (Fig. 5, crys) are found embedded in the exocuticle along its inner edge. They are flat prisms which are quite regular in size (9 x 4.5 x 2.5 microns). The crystals of *C. amyntor* are also found at the boundary between exocuticle and endocuticle. They are variable in size with the largest crystals having the dimensions of 20 x 5.5 x 2.5 microns.

The cuticle of the tomato and tobacco hornworms (*Phlegethontius quinquemaculatus* and *P. sexta*) is similar to that of *Ceratomia catalpae*. The crystals are embedded in the red-staining, untanned exocuticle. They are long prisms, a little longer and much narrower (9.5 x 2.2 x 2.2 microns) than those in the cuticle of *C. catalpae*.

The procuticle of *Sphinx chersis* (Fig. 6) is not differentiated into exo- and endocuticle. The crystals are small prisms (5 x 1 x 1 microns) scattered throughout the procuticle.

The procuticle of *Smerinthus* sp. is also undifferentiated. The crystals are about the same size and shape as those of *Sphinx chersis*, but they are located near the surface of the procuticle.

Four species of the family Nymphalidae were examined. *Nymphalis antiopa*, *Vanessa cardui*, and *Basilarchia archippus* have no crystals. *Polygonia interrogationis* has short prismatic crystals located in the procuticle just beneath the epicuticle. There are large numbers of small (3.3 x 1 x 1 microns) crystals in the intersegmental zone. Toward the middle of the segment the crystals become larger (6.7 x 2.3 x 2.3 microns) and fewer in number.

The only non-lepidopterous larva found to have calcium oxalate crystals in its cuticle was a hymenopteran, the birch leaf miner, *Fenusa pusilla*. Although six other tenthredinid species were examined, none was found to have crystals. The cuticle of *Fenusa* is very thin (10 microns). The crystal layer (Fig. 7, crys) is located just beneath the very thin epicuticle. The size (2.4 x 1.8 microns in surface view), shape, and location of the crystals are very similar to those of *Anisota*. The crystal layer is shed with the exuviae as it is in *Anisota*.

The one characteristic all of the crystal-bearing larvae have in common is that they are leaf-feeders. There is considerable variation in size, shape, and location of the crystals. The maximum crystal length ranges from 2–20 microns. The crystals are all prismatic, but vary from nearly cubical forms to long narrow prisms. They may be scattered throughout the cuticle (*Sphinx chersis*), but in most species are found embedded near the surface. The crystals are always absent from heavily tanned cuticular areas.

Since the families in which calcium oxalate crystals have been found show no close phylogenetic relationships, the ability of the epidermis to secrete calcium oxalate into the cuticle must have arisen a number of times in insect evolution. Secretion of calcium carbonate into, or beneath, the developing puparial cuticle is widely distributed among the phytophagous Diptera. The secretion of calcium into the cuticle is also found in many other arthropods (Crustacea, Arachnida, Diplopoda, Chilopoda). Calcium oxalate secretion by the epidermis of insect larvae may be a specialization of this more widely distributed epidermal calcium secretion.

REFERENCES

Campbell, F. L. 1929. The detection and estimation of insect chitin; and the irrelation of chitinization to hardness and pigmentation of the cuticula of the American cockroach, *Periplaneta americana* L. *Ann. Ent. Soc. Amer.* 22: 401–426.

Feigl, F. 1943. Laboratory manual of spot tests. *Academic Press*, New York.

Hallez, P. 1909. Les cristaux des Blattes. *C. R. Acad. Sci.* 148: 317.

Ito, H. 1924. Contribution histologique et physiologique à l'étude des annexes des organes génitaux des Orthoptères. *Arch. Anat. Micr.* 20: 343–460.

Pantel, M. J. 1919. Le calcium dans la physiologie normale des Phasmides (Ins., Orth.): oeuf et larve éclosante. *C. R. Acad. Sci.* 168: 127–129.

Wiesmann, R. 1938. Untersuchungen über die Struktur der Kuticula des Puppentönnchens der Kirschfliege, *Rhagoletis cerasi* L. *Vjschr. Schweiz. Naturf. Ges., Zürich*, Bleiblatt, 83: 127–136.

Wigglesworth, V. B. 1950. The principles of insect physiology. *E. P. Dutton Co.*, New York.

The Spiracular Gills of Insects

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ABSTRACT

Spiracular gills enable the pupa, or the adult enclosed within the pupal cuticle, to meet the contradictory demands presented by environments that are alternately dry and flooded. These structures have been independently evolved on a number of occasions in both the Coleoptera and Diptera. They exhibit great structural diversity and complexity. Some spiracular gills have a plastron. In others, the epidermis is isolated in the gill at the pupa-adult moult. Such tissue ceases to have any direct connection with the living animal and may be separated from it by considerable air-space. Wounds made in spiracular gills in which tissue is isolated are repaired by a plug of tanned protein. It has been found that wounds made in the spiracular gill of the pupal cuticle as long as five days after the emergence of the adult will be repaired. In the family Tipulidae such tissue-containing gills have been evolved independently on at least two occasions.

INTRODUCTION

All spiracular gills are modifications of the spiracle, or the integument of the body wall adjoining the spiracle, or both. So far as is known, they are confined to the pupal stage. Nevertheless, the spiracular gills of the pupal cuticle play an important part in satisfying the respiratory requirements of the young adult before it has shed the pupal cuticle. The metamorphosis of the pupa into the adult occurs some hours, days, or even months before the pupal cuticle is shed. Thus, the pupa-adult moult always occurs long before the pupal cuticle is actually shed, and during the interval between these two events the adult is only mechanically connected to the now dead pupal cuticle that envelopes it. The early part of the adult stage that is enclosed within the pupal cuticle is called the pharate adult stage (Hinton, 1946, 1948). It is only to be expected that amongst the structures of the pupal cuticle there are (1) those that function only during the pupal stage, (2) those that function during both the pupal and pharate adult stages, and (3) those that function only during the pharate adult stage. Amongst the latter are the mandibles of decticous pupae (Hinton, 1946a) and the swimming fringes of the legs of many trichopterous pupae. Spiracular gills are always functional in the pharate adult stage and in many species possibly also in the pupal stage. However, in *Lipsothrix*, and probably also in *Taphrophila*, the gills are functional only in the pharate adult stage because by the time that the larval cuticle is shed the pupa-adult moult has already occurred.

The significance of many of the structures of spiracular gills only becomes clear when they are seen not merely as structures adapted for respiration in water but as structures adapted both for the extraction of oxygen from the water and for atmospheric respiration. In water they provide a relatively enormous surface area for diffusion, and their structure is such that they do not collapse under the hydrostatic pressures to which they are normally subject. When the pupa or pharate adult is out of the water, the gill does not involve the animal in water loss over an enormous surface because the connection between the lumen of the gill and the internal tissues of the animal is restricted to a surface hardly if at all greater than that of the spiracles of terrestrial insects. Thus a spiracular gill not only provides an enormous surface area for extraction of oxygen from the water, but in air the total surface area for humidity exchanges between the saturated air in the tracheae and the drier air outside is about as restricted as in any insect with normally formed spiracles.

In most species the total surface area of the spiracular gills is such that we may suppose that no limit is set upon the degree of impermeability that may be attained by the body-wall cuticle. By making use of the flagellate, *Bodo sulcatus*, Fox (1921) found that *Simulium* absorbed no oxygen through its body-wall cuticle but only through its spiracular gills. In other species, e.g. the Tipulidae, the body-wall cuticle is to some extent permeable but figures are not available to show for any one species the proportion of the oxygen demand satisfied by diffusion through the body-wall cuticle and through the spiracular gills.

CONTROL OF WATER LOSS

When the insect is exposed above water, the problem of water loss through the spiracles does not differ from that of terrestrial insects. In pupae of terrestrial insects, the muscles of the regulatory apparatus of the larva are carried over directly and become inserted in the regulatory apparatus of the pupa. In the pharate adult stage it would appear that the regulatory apparatus functions more or less normally despite the fact that the pupal trachea is enclosed within the adult trachea. In diapausing pupae in which cytochrome *c* and cytochrome oxidase virtually disappear from most tissues, the muscles of the regulatory apparatus are shielded from the action of the diapause hormone as are some of the skeletal muscles of the abdomen. But both the Psephenidae (Hinton, 1955) and all Diptera (Hinton, 1953) are derived from ancestors that had secondarily lost a spiracular regulatory apparatus in the larval stage. It therefore follows that prevention of water loss through the spiracles when they are exposed above water must be solved in some other way by all insects that have spiracular gills.

In the genus *Psephenoides* a spiracular regulatory apparatus is present in the pupa, but muscles are not inserted in it. At the pupa-adult moult a similar regulatory apparatus is formed and muscles developed during the pupal period are inserted in it. But the spiracular atrium of this genus has a long "felt" chamber of very fine and dense cuticular processes: the felt chamber of *P. volatilis* Champ. is 1/6 and that of *P. gahani* Champ. is 1/10 as long as the pupa (Hinton, 1947a). By analogy with what is known of similar felt chambers in dipterous larvae, we may suppose that those of *Psephenoides* serve to establish an effective humidity gradient.

In the Tipulidae with spiracular gills (Hinton, 1955a, 1957), the cuticular processes of the walls of the atrium would slow down the flow of air by pressure resistance and frictional drag, but they are too far apart to be compared with the "felting" of *Psephenoides* and many dipterous larvae. However, in these Tipulidae the pupal stage is either completed before the larval cuticle is shed or a few hours afterwards, and regulation of water loss after the larval cuticle is shed may be chiefly dependent upon the regulatory apparatus of the adult spiracles. The regulatory apparatus of the thoracic spiracles of all adult Diptera is similar: it consists of two lips that are pulled together when the single occlusor muscle contracts. It is not known to what extent, if any, the enclosed pupal trachea affects the efficiency of the apparatus. It would seem that the secondary loss of a spiracular regulatory apparatus in the larval stage thus places a premium upon the completion of the pupal stage before or very shortly after the larval cuticle is shed.

In the Simulidae, however, the problem of water loss is solved in an altogether remarkable fashion. In this family there are *two* regulatory systems in the pharate adult stage. The first of these is the usual regulatory apparatus of the adult. The second is a "bow" type of regulatory apparatus at the distal end of the spiracular atrium immediately behind the base of the spiracular gills. The existence of this apparatus has been noted by Pulikovsky (1927). The muscle that moves the lever of the regulatory apparatus of the pupal spiracle lies within the haemocoele of the adult; it is separated from the pupal spiracle by the cuticle of the adult and a layer of moulting fluid. The apodeme on which it is inserted very closely ensleaves an apodeme of pupal cuticle. The pupal apodeme is the backward extension of the lever of the regulatory apparatus of the pupal spiracle. Before it reaches the adult apodeme, the pupal apodeme extends through a delicate epithelial sleave which is a modified part of the epidermal layer of the body wall of the adult. As the adult is emerging from the pupal cuticle, the pupal apodeme is broken off and pulled out of the epithelial sleave. The epithelial sleave, which looks like a thin papilla projecting out of the side of the thorax of the adult above the first thoracic spiracle, is withdrawn into the thorax during the process of emergence. Judging from the appearance of the broken end of the pupal apodeme, it would seem possible that some of it is left enclosed in the adult apodeme and thus retained in the body of the adult. In this connection it is of interest to note that Satchell (1948) has described a similar regulatory apparatus, also with a muscle projecting out of the side of the thorax of the adult, in the Psychodidae.

DISTRIBUTION OF SPIRACULAR GILLS

Spiracular gills are structures that enable the immobile or relatively immobile pupa or pharate adult of some insects to meet the contradictory demands presented to them by environments that are alternately dry and flooded. It thus seems to be no accident that spiracular gills are largely confined to pupae that inhabit rapidly flowing streams, since one of the most characteristic features of such streams is the rapid fluctuation of the water level. Spiracular gills occur in beetles of the family Psephenidae and in the following families of Diptera: all Simulidae, Blepharoceridae, Deuterophlebiidae, some Chironomidae, some Hemerodromiinae (Empididae) and some Limoniinae (Tipulidae). Spiracular gills also occur in some Chironomidae that do not pupate in streams but live in ponds and lakes. When these are shallow the pupae may be exposed to alternate flooding and drying. Of significance in this connection is the fact that intertidal Tipulidae have spiracular gills.

In the Psephenidae spiracular gills are present only on abdominal segments 2–7. In the Empididae they are present on the prothorax and abdominal segments 1–7, and in all other Diptera only on the prothorax. When spiracular gills are present, the spiracles of segments other than those bearing spiracular gills are, so far as is known, always non-functional. The so-called "prothoracic" spiracles of the Diptera and all other insects are the mesothoracic spiracles that have secondarily migrated on to the prothorax, as is quite clear from both embryological and phylogenetic evidence (Hinton, 1947). The tracheo-spiracular metamere of the mesothorax is not lost as is sometimes claimed (*e.g.* Keilin, 1944).

CLASSIFICATION OF SPIRACULAR GILLS

A natural classification of spiracular gills is precluded because they have been independently evolved in each group of insects. Their structural diversity is so great that it is not at all easy to group them according to structure even while recognizing the fact that similarities of structure between different families (and sometimes even within families) are the result of convergence or parallelism and not an indication of phylogenetic relationship. When to all this is added the fact that little is known of the functional significance of many of the structures of the gills of even the more common species, *e.g.* Chironomidae, the classification now proposed cannot be regarded as more than a preliminary one.

I. Blood and epidermis not isolated in spiracular gill at pupa-adult moult, or if so isolated soon degenerates (Simuliidae).

  A. Spiracular gills formed entirely by body-wall adjacent to spiracle. The spiracle itself does not extend beyond the general level of the body wall.

    1. Without plastron.
        None known.

    2. With plastron.
        Simulidae.
        Deuterophlebiidae.
        Blepharoceridae: *Blepharocera*, *Liponeura*, *Horaia*, *Cuprina*, *Paracurupira*, *Kelloggina*, *Peritheates*.
        Empididae: some Hemerodromiinae,

  B. Spiracular gills formed by the body-wall adjacent to the spiracle and the spiracle itself. The atrium of the spiracle extends into the spiracular gill beyond the general level of the body wall.

    1. Without plastron.
        Psephenidae: Psephenoidiinae, some Eubriinae.
        Chironomidae: many Chironominae.

    2. With plastron.
        Blepharoceridae: many (all ?) species of *Edwardsina*, *e.g. E. similis* Tonn. and *E. gracilis* Edw.

II. Blood and epidermis isolated in spiracular gill at pupa-adult moult by a basal membrane. Isolated tissue competent to repair injuries to spiracular gill with tanned cuticle during life of pharate adult and for some days after emergence of adult.

  A. After pupa-adult moult epidermis becomes syncytial and remains attached to cuticle. Plastron does not resist a pressure difference of more than a few cm.
        Tipulidae: Eriopterini (*Lipsothrix*).

B. After pupa-adult moult epidermis of parts of the gill dissociates: the cells become rounded and separate away from one another and from the cuticle. Plastron resists a pressure difference of about 0.3 atm.

Tipulidae: Limoniini (*Taphrophila*, *Geranomyia*).

The distinction between "IA" and "IB" is not always of much significance. For instance, in *Edwardsina gracilis* Edw. and many other species of the genus, the spiracular atrium extends into the gill far beyond the general level of the body-wall, whereas in *E. dispar* Edw. the gill is much shorter and the spiracular atrium scarcely extends beyond the level of the body-wall. Pupae of *Euliponeura* and several other unusual Blepharoceridae have not been available, nor has it been possible on the basis of published descriptions to enter them in the preliminary classification given above. Some Telmagetonini (Clunioninae), e.g. *Telmageton*, *Paraclunio*, and some (*T. frauenfeldi* Schiner) but not all species of *Thalassomyia*, have large flattened structures that appear to be spiracular gills, but the spiracular atrium is not dilated as it is in the Limoniini of comparable structure. If the structures of the Telmagetonini are indeed spiracular gills, they belong to the category "IBI" but are very much simpler than those of the Chironominae and have been independently evolved. I am aware of no adequate description of the complex spiracular gills of the Chironominae.

The existence of a plastron in the Blepharoceridae has not previously been recognized, but all genera cited in the list given above appear to have a plastron. Only material preserved for many years has been available, and therefore the existence of a plastron in this family requires confirmation from experiments on fresh or living animals. The plastron of the Simulidae will be described in detail in a later paper, and it is here only necessary to state that the cuticular processes of the gill walls are not enclosed in a continuous membrane as claimed by Taylor (1902).

The isolation of tissue in the spiracular gill at the pupa-adult moult has only recently been discovered (Hinton, 1955a), and I suspect the phenomenon will be found to be not uncommon, so that some groups now listed in "I" may have to be removed to "II".

THE TISSUE ISOLATED IN THE GILLS OF THE TIPULIDAE

All Tipulidae with spiracular gills are derived from terrestrial species with respiratory horns, and there seems to be little doubt that the spiracular gills of the three genera of Tipulidae (*Lipsothrix*, *Geranomyia*, *Taphrophila*) are of independent origin. The plastron of each is also evolved independently. The structure of that of *Taphrophila* (Limoniini) is similar to that of *Lipsothrix* (Eriopterini) and very different from that of *Geranomyia* (Limoniini). Only the efficiency of the plastron of *Taphrophila* has been adequately tested (Hinton, 1957): it is not wetted at pressures less than about a third of an atmosphere above normal, and it is only wetted by surface active substances that reduce the surface tension to about 25 dynes/cm.

In all terrestrial or subaquatic species of *Limonia*, *Dicranomyia*, and *Helius* that were examined, blood and epidermis are isolated in the respiratory horns at the pupa-adult moult. No tissue was found in the respiratory horns of *Thaumastoptera calceata* Mik., but the few pupae available were poorly preserved. From present evidence it would appear that the isolation of tissue in the respiratory horns at the pupa-adult moult is common to all Limoniini, and that the phenomenon is therefore not of independent origin in the spiracular gills of *Taphrophila* and *Geranomyia*. No isolated tissue was found in the respiratory horns of the terrestrial Eriopterini examined: species of *Ellipteroides*, *Gonomyia*, *Gonempeda*, *Platytoma*, *Erioptera*, *Symplecta*, *Ilisia*, *Ormosia*, *Scleroprocta*, *Rhypholophus*, *Molophilus*. Thus, since the sub-aquatic *Lipsothrix* is derived from a terrestrial species of Eriopterini, it seems clear that the isolation of the tissue at the pupa-adult moult has arisen at least twice independently within the family Tipulidae.

The attributes of the tissue isolated in the spiracular gills of *Lipsothrix remota* Walk. and *Taphrophila vitripennis* Meig. have recently been described in some detail (Hinton, 1957). During the pharate adult stage the tissue isolated in the spiracular gills is separated from the living animal by two cuticles—the basal membrane and the adult cuticle—between which is the moulting fluid. The duration of the pharate adult stage of both species is 8–9 days at 18–20°C. During the whole of this time small holes or cuts made through the walls of the spiracular gills are repaired with plugs of dark amber to black cuticle. For

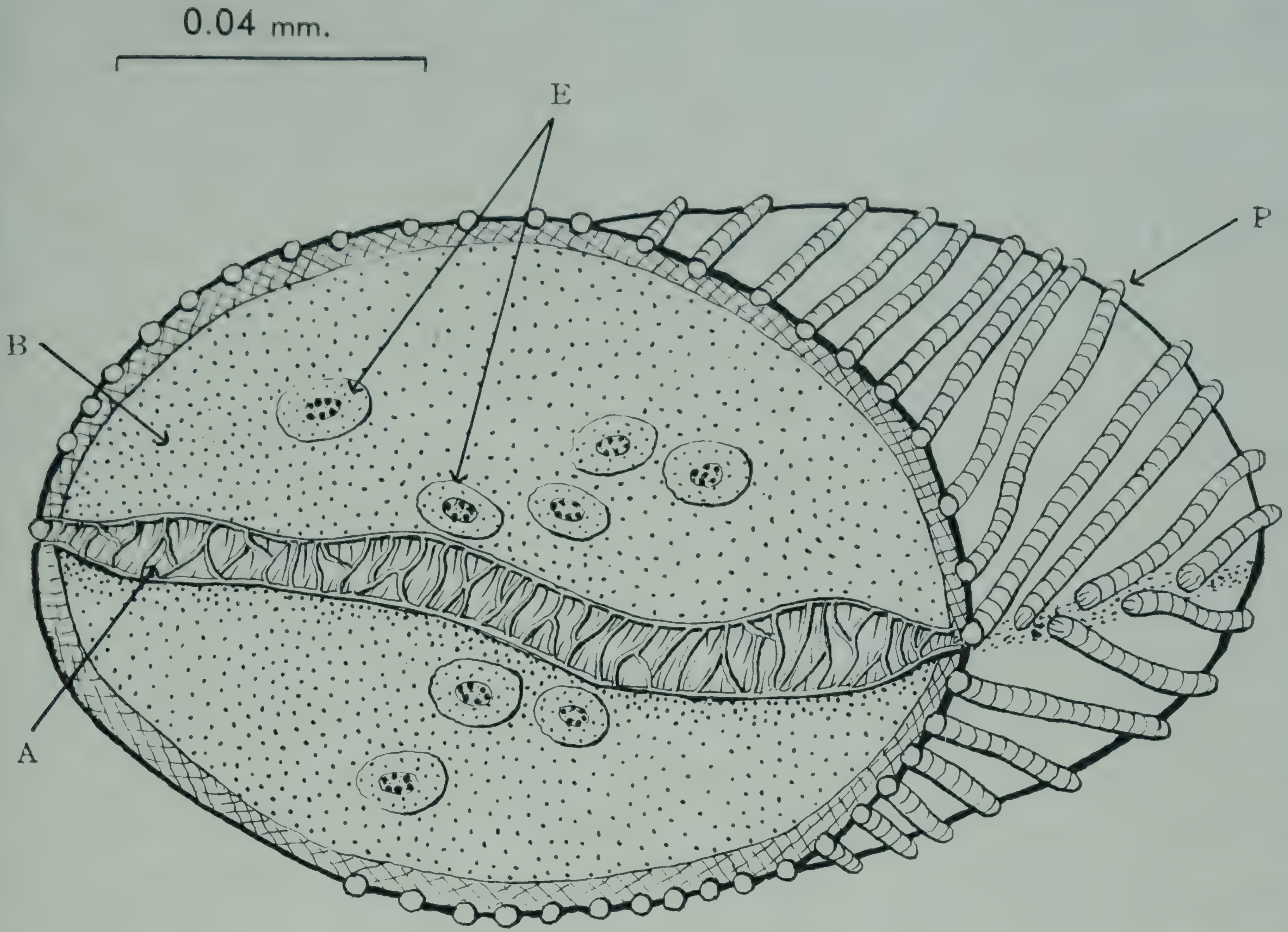

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Fig. 1. *Taphrophila vitripennis* Meig., pharate adult stage after dissociation of epidermis is completed. Section through common base of apically clubbed branch and first dorsal branch, semi-diagrammatic. (A) Spiracular atrium; (B) cell-free blood: no haemocytes appear to be isolated in the gill; (E) epidermal cells that come to resemble haemocytes; (P) plastron line.

instance, in one experiment the inner external wall of each of 84 gills of *Lipsothrix* was pierced through with a fine needle in three places, and 96% of the gills repaired the wounds with a plug of dark cuticle. The plug material is sclerotin: it withstands prolonged periods in concentrated nitric or hydrochloric acid, it is rapidly dispersed in concentrated nitric acid saturated with potassium chlorate, and its formation is completely inhibited by phenylthiourea.

At 18–20°C the tissue isolated in the pupal gills of both species retains its competence to repair wounds up to five days after the adult sheds the pupal cuticle. For instance, in one experiment 5 of 23 gills of *Lipsothrix* repaired wounds made from 97 to 120 hours after the emergence of the adult.

The 8-branched gill of *Taphrophila* quickly dries and collapses out of water. At 65% R. H. there is a general collapse of all branches in 9 minutes. When a dry gill is immersed in water, the isolated tissue absorbs water and the branches quickly become turgid. The isolated tissue is competent to repair injuries to the gill wall after it has been dried. The isolated epidermal cells will tolerate dehydration to $<1\%$ moisture content. The tissue in gills kept as long as 70 days over phosphorus pentoxide repaired injuries made after the gills were again immersed in water. When dry the epidermis will tolerate high temperatures. That of gills dried for various periods up to 70 days over phosphorus pentoxide and heated when dry to 103°C for 2 hours or 130°C for 30 minutes repaired wounds made when it was re-hydrated.

The capacity to tolerate complete dehydration is not peculiar to the epidermis isolated in the spiracular gill. The epidermis of the larva and adult of *Taphrophila* has a similar capacity. Larvae and adults die when they lose 10–20% of their moisture content, but, if the drying be rapid, the epidermis survives and can be dried as long and heated as much as that isolated in the gill. However, when placed in water or Ringer after a period of drying, or both drying and heating to over 100°C, the epidermis rather rapidly loses its capacity to form plugs of sclerotin: no wounds were repaired that were made as long as 40 hours after re-hydration. The reason for this may be that in water the epidermis is soon poisoned and killed by the products of decomposition of the tissues that did not survive the dehydration.

Preliminary experiments suggest that the epidermis of a great many insects can tolerate dehydration to $<1\%$ moisture content for prolonged periods. When larvae of Chironomidae and various beetles (Gyrinidae, Haliplidae, Elmidae, Psephenidae) were dried for periods of 12 to 692 hours over phosphorus pentoxide, the epidermis of all repaired wounds made after they were re-hydrated for 4 to 24 hours. All of these insects die when their moisture content falls about 20%. Attempts to repeat these results on the cockroach have not been successful, perhaps because its cuticle is too impermeable and its tissues cannot be dried as fast as those of aquatic insects with much more permeable cuticles. The capacity of other tissues to survive total dehydration is much less common, and only two species of insects are known that will grow after total dehydration: the larva of *Polypedilum vanderplanki* Hint. (Chironomidae) and that of an unidentified Ceratopogonid (Hinton, 1951, 1953).

REFERENCES

Fox, H. M. 1921. Methods of studying the respiratory exchange in small aquatic organisms, with particular reference to the use of flagellates as an indicator for oxygen consumption. *J. gen Physiol.* 3: 565–573, 5 figs.

Hinton, H. E. 1946. Concealed phases in the metamorphosis of insects. *Nature*, Lond. 99: 552–553, 1 fig.

Hinton, H. E. 1946a. A new classification of insect pupae. *Proc. zool. Soc. Lond.* 116: 282–328, 64 figs.

Hinton, H. E. 1947. On the reduction of functional spiracles in the aquatic larvae of the Holometabola, with notes on the moulting process of spiracles. *Trans. R. ent. Soc. Lond.* 98: 449–473, 5 figs.

Hinton, H. E. 1947a. The gills of some aquatic beetle pupae (Coleoptera, Psephenidae). *Proc. R. ent. Soc. Lond.* (A) 22: 52–60, 1 pl., 12 figs.

Hinton, H. E. 1948. The origin and function of the pupal stage. *Trans. R. ent. Soc. Lond.* 99: 395–409, 1 fig.

Hinton, H. E. 1951. A new chironomid from Africa, the larva of which can be dehydrated without injury. *Proc. zool. Soc. Lond.* 121: 371–380, 1 pl., 5 figs.

Hinton, H. E. 1953. Some adaptations of insects to environments that are alternately dry and flooded, with some notes on the habits of the Stratiomyidae. *Trans. Soc. Brit. Ent.* 11: 3 figs.

Hinton, H. E. 1955. On the respiratory adaptations, biology, and taxonomy of the Psephenidae, with notes on some related families (Coleoptera). *Proc. zool. Soc. Lond.* 125: 543–568, 30 figs.

Hinton, H. E. 1955a. The structure of the spiracular gill of the genus *Lipsothrix* (Tipulidae), with some observations on the living epithelium isolated in the gill at the pupa-adult moult. *Proc. R. ent. Soc. Lond.*(A) 30: 1–14, 14 figs.

Hinton, H. E. 1957. The structure and function of the spiracular gill of the fly *Taphrophila vitripennis*. *Proc. Roy. Soc.* (B) 147: 90–120.

Keilin, D. 1944. Respiratory systems and respiratory adaptations in larvae and pupae of Diptera. *Parasitology* 36: 1–66, 2 pls., 54 figs.

Pulikovsky, N. 1927. Die Respiratorischen Anpassungserscheinungen bei den Puppen der Simuliiden (und einigen anderen in schnellfliessenden Bachen lebenden Dipterenpuppen). *Z. morph. oekol. Tiere* 7: 384–443, 31 figs.

Satchell, G. H. 1948. The respiratory horns of *Psychoda* pupae (Diptera: Psychodidae). *Parasitology* 39: 43–52, 27 figs.

Taylor, T. H. 1902. On the tracheal system of *Simulium*. *Trans. ent. Soc. Lond.* 1902: 701–716, 8 figs.

A Simple Method for Sexing Living *Anopheles* Larvae

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ABSTRACT[1]

Third stage Anopheles quadrimaculatus *Say larvae (LTD strain) may be sexed with about 90% accuracy by differences in body pigmentation. Black, heavily pigmented larvae usually develop into females; light, poorly pigmented third instars usually develop into males.*

Fourth instar Anopheles *can be sexed with 100% accuracy throughout the stadium by examination of the imaginal antennal discs. Male larvae have well-developed antennal discs with large torus-forming part. Females have poorly developed antennal discs with small torus-forming part.*

The anatomy of the antennal discs is described and the early developmental stages compared.

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The Tergal Depressor of the Trochanter Muscle in the Diptera

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ABSTRACT

The results of a survey of representatives of about two-thirds of the families in the Order Diptera for the presence or absence of the Tergal Depressor of the Trochanter Muscle (synonyms listed in Table I) are reported. Some tentative systematic and phylogenetic conclusions are reached as a result of the survey.

The muscle here called the Tergal Depressor of the Trochanter (Maki, 1938) (abbreviated as TDT-muscle below) is a distinctive muscle originating on the tergum of the mesothorax and inserting on the trochanter of the leg of the same segment. On contracting this muscle pulls on the trochanter on the proximal side of the axis of the coxal-trochanteral articulation and so depresses the femur to which the trochanter is fused.

In Table I are listed some of the names by which various authors have designated the TDT-muscle.

TABLE I. Synonyms of Tergal Depressor of Trochanter Muscle.

Maki	(1938)	"Tergal depressor of Trochanter", in Diptera and other Insects.
Ritter	(1911)	"Fourth dorso-ventral muscle" or "trochanter muscle", in *Calliphora.*
Bonhag	(1949)	"Depressor of Trochanter", in *Tabanus.*
Miller in Demerec	(1950)	"Extra-coxal depressor of Trochanter", in *Drosophila.*
Hasken	(1939)	"Dorso-ventral muscle 3", in *Panorpa.*
Weber	(1928, etc.)	"Dorso-ventral muscle 4–7", in *Papilio*, etc.
Nuesch	(1953)	"Tergal depressor of Trochanter", in *Telea.*
Snodgrass	(1935)	"Extra-coxal depressor of Trochanter", in text-book description based largely on *Dissosteira.*
Carbonell	(1947)	"Tergal branch of main depressor of the leg", in *Periplaneta.*
Albrecht	(1953)	"Depressor of Trochanter", in *Locusta.*
Whittig	(1955)	"Tergo-endocoxalis muscle", in *Perla.*
Matsuda	(1956)	"Noto-Trochanteral muscle", in *Blatella* and *Agulla.*

Carbonell (1947) described the TDT-muscle in the American Cockroach, *Periplaneta americana* (Linn.), as a single muscle. Snodgrass (1952) agreed with Carbonell's description. Snodgrass (1935), in a textbook description based largely on the conditions in the Grasshopper *Dissosteira carolina* (Linn.), described the TDT-muscle in a winged segment as single. In addition a muscle runs from the same insertion on the trochanter to the basalar plate.

In *Panorpa* (Mecoptera) Hasken (1939) has shown that the TDT-muscle in both meso- and meta-thoraces is single as in *Periplaneta.* The basalar slip noted above is present but Hasken, erroneously, thought that it inserted on the coxa instead of the trochanter.

When present in Diptera the TDT-muscle is a single bundle; the basalar slip is lost throughout the Order. As pointed out by Miller in Demerec (1950), the TDT-muscle differs in structure (as seen in transverse sections) from the longitudinal and dorso-ventral indirect flight muscles; it resembles the direct wing-base muscles on the pleural wall and those associated with the legs. When well developed in the mesothorax of Diptera it assumes a fanned-out shape at its origin on the tergum. TDT-muscle in Diptera often has a slightly different superficial appearance when compared with the big indirect flight muscles; it is of the same appearance as the other smaller muscles noted above which it resembles in transverse section. This suggests that the TDT-muscle in the Diptera is a tetanic or "slow" muscle rather than a twitch or "fast" one. This disassociation from the great indirect flight muscles of the Dipteron mesothorax is confirmed by Zalokar's (1947) findings. Zalokar, reporting on ablation experiments using pupae of *Drosophila*, indicated that, as an organ, the TDT-muscle was associated with the ventral or leg imaginal-disc and not with the dorsal or wing imaginal-disc with which the indirect flight muscles were, in fact, associated.

Maki (1938) noted that this TDT-muscle was not present in all Diptera. He found it present in a Stratiomyiid of the sub-family Beridinae, a Syrphid, a Calobatid and a Muscid but absent from a Tipulid. Tiegs (1950) reported briefly on the presence or absence of the muscle in representatives of twelve families of Diptera. Prior to the appearance of Tieg's paper I had noted the absence of the muscle in *Anisopus fenestralis* (Scop.) and it was, in fact, this absence that originally attracted my attention to the matter of this muscle in the mesothorax of Diptera. Published information was thus available about the TDT-muscle in representatives of fourteen families of Diptera with Anisopidae as a fifteenth.

I decided to make a survey of the Diptera to see if the presence or absence of the TDT-muscle had any taxonomic value or possible phylogenetic significance and have now examined representatives of some forty-two of the approximately sixty-five families usually recognised in the less diffuse classifications of Diptera.

The survey is not complete.[1] An attempt has been made to concentrate on groups whose taxonomic history indicated possible cleavages (e.g. Tabanidae) or where there were forms that are usually considered to be of interest from the phylogenetic point of view (e.g., Anisopidae) (Crampton, 1942; Edwards, 1926; Edwards & Keilin, 1928). No attempt has been made to cover the families of the Acalypterate Cyclorrhaphous Diptera, or the various sub-families of families which are isolated in systematic position (e.g., Empididae, Dolichopodidae). Otherwise availability of material was the criterion for inclusion.

The TDT-muscle is not the only muscle inserting on the same tendon and acting as a depressor of the trochanter. Some originate on the wall of the coxa. A large one originates on the furca. Some Diptera have a muscle with its origin on the pleural apodeme. Maki (1938) found that this muscle, originating on the pleural apodeme, was present in the Tipulid and absent in the other four Diptera that he investigated; this suggests that there may be a correlation between its presence and or absence and that of the TDT-muscle. A complete survey would, therefore, need to include data on this and other muscles as well as noting the presence or absence of the TDT-muscle itself.

The results of the survey are shown in Table II.

Though the survey is incomplete, examination of Table II suggests a few comments.

1. Presence or absence of the TDT-muscle is not coincident with any of the usual lines along which the Diptera are usually divided by systematists. It can, furthermore, be assumed that forms which lack the TDT-muscle cannot be ancestors of forms in which the TDT-muscle is present.

2. A surprisingly large number of Nematocera lack the TDT-muscle and among them the presence or absence seems characteristic at the family level. This suggests that the muscle was lost well back in the sub-Order's history either by groups that have since become isolated as families or, perhaps, at one point dividing the Nematocera into two streams, the one with and the other without the muscle. The four families noted as having the TDT-muscle are all rather active forms that run over the ground on their legs when not flying. They have certain other community of features such as well developed coxae and, except in Sciaridae, biting mouth-parts. They are sturdy, though small, flies, compared with most of those that lack the TDT-muscle. All the delicate long-legged Nematocera

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[1] The following listing is an indication of Diptera that the writer feels most anxious to examine and/or get information about the condition of the TDT-muscle:—

Tanyderidae, *Bittacomorpha*, *Bruchiomyia*, *Olbiogaster*, *Bolitophila*, Hesperinidae, Pachyneuridae, Corynoscelidae, Nymphomyiidae, Deuterophlebidae.

Those rare genera of "lower" Brachycera whose assignment in classifications ranges over the following families:—Stratiomyiidae, Errinidae, Solvidae, Rachiceridae, Coenomyiidae, Rhagionidae and Tabanidae.

Pantophthalmidae, Sciadoceridae, Nemestrinidae, Oncodidae, Platypezidae, Mydaidae.

Conopidae, Pyrgotidae, Pallopteridae, *Sphyrocephala*.

Dermatobia, *Pseudogametes*, *Alouattamyia*, *Bogeria*, *Rodhainomyia*, *Pharynyngomyia*, *Cephenomyia*, *Cephalopsis*, *Hippoestrus*, *Rhinoestrus*, *Pharyngobolus*, *Dermatoestrus*, *Oedamagena*, *Oestromyia*, *Gyrostigma*, *Rhinogogastrophilus*.

Hippoboscidae, Nycteribiidae and Streblidae.

Cyclorrhapha, Calypteratae and Acalypteratae: The families and more especially the genera which might be of interest are so numerous that it is impracticable to list them other than the few mentioned above. Apterous or brachypterous species, or any with specialised flying habits, would, however, be of especial interest.

Specimens can be killed in strong alcohol (90+%, industrial or commercial methylated spirits, etc.), left in it for 24 hours or so and stored in 70% alcohol. Better is to fix in Picro-Chlor-Acetic fixative (12 vols. 1% solution of Picric Acid in 90+% Alcohol, or industrial methylated spirits + 2 vols. chloroform + 1 vol. glacial acetic acid; the mixture keeps satisfactorily) for 12 hours (or over-night) and store in 70% alcohol after leaving in at least one change of 70% alcohol for 24 hours. The consequent yellow staining of the tissues is no disadvantage. Alternatively other fixatives and preserving fluids that will quickly penetrate the insect's cuticle and harden the tissues are suitable. Preserving fluids that are intended to leave the tissues soft and flexible are not as satisfactory, for purposes of examining the musculature, as fluids which harden the tissues.

fall in the group that lack the TDT-muscle; they are forms that one thinks of as flying rather like helicopters and being inactive on the ground when not flying. Most of the highly specialised Nematocera fall in this second group.

TABLE II. Tergal Depressor of Trochanter Muscle in Diptera.

PRESENT IN:–	ABSENT IN:–	
Simuliids	*Trichocera*	*Anisopus*
Sciarids	Tipulids*	*Mycetobia*
Psychodids*	*Ptychoptera*	*Thaumalea*
Nemopalpus (Psychodid)	Culicids	Mycetophyliids
	Chironomids*	Cecidomyiid
	Blepharocerid	Bibionids
Hermetia (Stratiomyiid)	Stratiomyiids*	
*Tabanus**, *Haematopota*, *Chrysops*	*Pangonia*	
Rhagionids*, Therevid*, Scenopinid	*Coenomyia*	
Exoprosopa (Bombyliid)	*Bombylius**	
Empids, Dolichopodids	Asilids*	
Lonchopterid, Phorid, Syrphids*	Pipunculids	
Conopid		
Dryomyza, and other Acalypterates*	*Gasterophilus*	
*Calliphora**, *Sarcophaga*, Tachinid*		
Oestrus, *Hypoderma*, *Cuterebra*		
Scatophagid, Muscids*, *Stomoxys*	*Glossina*, *Hippobosca*	

*Reported by previous workers.

It is interesting to note that both Anisopidae (*Anisopus fenestralis* (Scop.) dissected) and Trichoceridae (*Trichocera* sp. dissected), both of which have been considered as primitive and of phylogenetic significance by various authorities, lack the TDT-muscle. It would be particularly interesting to have been able to report on the condition of the muscle in *Protoplasa* and/or *Tanyderus* (see footnote).

3. The groups differentiated on the presence or absence of the TDT-muscle in the Brachycera (Brachycera-Orthorrhapha *auctt.*) are both at the family and the sub-family level. Unless the information is to be used to completely upset the present concepts of the families in the Brachycera, it must be concluded that the TDT- muscle has been lost on several separate occasions in the phylogenetic history of the Brachycera.

That sub-family groups differ from each other in this feature in Bombyliidae, Stratiomyiidae and Tabanidae is a warning against hasty conclusions on the basis of too few representatives of a family. It might, perhaps, be suggested that the TDT-muscle seems to be lost amongst specialised rather than less-specialised forms of Brachycera.

It is interesting to note that recently, reviewing the systematics of the Tabanidae, Mackerras (1954) separated the group comprising *Pangonia* and its obvious relatives from the groups in which would contain *Tabanus*, *Haematopota* and *Chrysops*. *Coenomyia* lacks the TDT-muscle while representatives of Rhagionidae(=Leptidae *auctt.*) examined possessed the muscle. This suggests that information about the condition of the TDT-muscle in the genera of these so-called "lower" Brachycera might aid in their classification. Unfortunately many of these are very rare (see footnote) as collected material especially in a condition suitable for dissection of the musculature.

4. The bulk of the Cyclorrhapha (Brachycera-Cyclorrhapha *auctt.*) appear to possess a TDT-muscle. The exceptions are interesting in that they are all specialised, rather isolated systematically and, to judge by their habits, presumably relatively recently evolved groups with few genera in the family segregates in which they are usually placed.

5. In the Cyclorrhapha Aschiza the Pipunculidae whose representatives proved to lack the TDT-muscle are a group which have very specialised habits correlated with their parasitic mode of life as larvae.

6. In the Cyclorrhapha Schizophora all the relatively few Acalypterates examined, except *Gasterophilus*, had the TDT-muscle present and in many cases very well developed.

It is, however, possible that *Gasterophilus* is not yet correctly placed in the general classification of Diptera. In this connection it is worth noting (see below) that members examined of the family Oestridae, as it used to be considered, have the TDT-muscle extremely small.

7. The information about the Calypterate Cyclorrhapha Schizophora is interesting. *Oestrus*, *Cuterebra* and *Hypoderma* have the TDT-muscle but it is very weakly developed. This suggests, especially when the condition in *Gasterophilus*, *Glossina* and *Hippobosca* is taken into consideration, that there is some correlation between the lack of the TDT-muscle and specialised habits of the imagines. Information about some of the rare and diverse genera usually grouped in the "Oestrids" in the wide older sense would be of considerable interest (see footnote).

Glossina lacks the TDT-muscle and is thereby brought into association with the viviparous *Hippobosca* and separated from *Stomoxys*. In older systematic work attempts were sometimes made to associate *Glossina* with the Pupipara *auctt.* (viz families Hippoboscidae, Streblidae, Nycteribiidae and Braulidae of the Schizophorous Cyclorrhapha) because of the viviparous habit rather than with *Stomoxys* and related flies with which it shared the habit of sucking blood by wounding with the thecate labium.

8. When all the above facts are kept in mind it is obvious that the disappearance of the TDT-muscle must have taken place over and over again in the Phylogenetic history of the Order Diptera. It is out of the question, when other anatomical facts are kept in mind, to suggest that there have been two streams of evolution in the Diptera—one with and one without the TDT-muscle. The function of the TDT-muscle in flight is not clear. On the ground it could help flies with suitable legs to leap into the air. In flight, with the legs hunched up, it could be used to distort the thorax mesothorax and so influence the flight of the insect.

Not enough is known of the flight and other habits of many Diptera. Certainly separation of flies into those with and those without the TDT-muscle does not coincide with groupings, based on types of flight, recently suggested by Rohdendorf (1951).

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REFERENCES

Albrecht, F. O. 1953. The anatomy of the migratory locust. *Univ. Lond. Athlone Press*, London.

Bonhag, P. F. 1949. The thoracic mechanism of the adult horsefly (Diptera: Tabanidae). *Cornell. Univ. Agric. Expt. Stn., Mem.* 285: 1–39.

Carbonell, C. S. 1947. The thoracic muscles of the cockroach *Periplaneta americana* (L.). *Smiths. Misc. Coll.* 107(2): 1–23.

Crampton, G. C. 1942. The external morphology of the Diptera. *Guide to the insects of Connecticut* 6(1): 10–165.

Edwards, F. W. 1926. The phylogeny of nematocerous Diptera: a critical review of some recent suggestions. *III Internat. Ent. Congr.*, Zurich, 1925, Bd. 2: 111–130.

Edwards, F. W., & D. Keilin. 1928. Diptera Fam. Protorhyphidae, Anisopidae, Pachyneuridae, Trichoceridae. *Genera Insectorum*, Fasc. 190: 1–41.

Hasken, W. 1939. Der thorax von *Panorpa communis* L. *Zool. Jahrb. Anat. u. Ont.* 65: 295–338.

Mackerras, I. M. 1955. The classification and distribution of Tabanidae (Diptera). II. History: Morphology: Classification: Subfamily Pangoniinae. *Aust. Jl. Zool.* 3(3): 439–511.

Maki, T. 1938. Studies on the thoracic musculature of insects. *Mem. Fac. Sci. Agr. Taihoka Imp. Univ.* 24(1): 1–343.

Matsuda, R. 1956. The comparative morphology of the thorax of two species of insects. *Microentomology* 21(1): 1–65.

Miller, A. 1950. *In* Demerec, Biology of Drosophila. *Witez*, New York; *Chapman & Hall*, London.

Nuesch, H. 1953. The morphology of the thorax of *Telea polyphemus* (Lepidoptera). *Jl. Morph.* 93(3): 589–607.

Ritter, W. 1911. The flying apparatus of the blow fly. A contribution to the morphology and physiology of the organs of flight in insects. *Smiths. Misc. Coll.* 56(12): 1–76.

Rohdendorf, B. B. 1951. Organs of locomotion of two-winged insects and their origin. (Entirely in Russian). *Trud. paleont. Inst. SSSR*, Moscow, 35: 1–179.

Snodgrass, R. E. 1935. Principles of insect morphology, *McGraw-Hill Book Co.*, New York & London.

Snodgrass, R. E. 1952. A textbook of arthropod anatomy. *Comstock Publishing Co.*, Ithaca, N.Y.; *Constable*, London.

Tiegs, O. W. 1955. The flight muscles of insects—their anatomy and histology; with some observations on the structure of striated muscle in general. *Phil. Trans. R. Soc. Lond.*, B., (656) 238: 221–359.

Weber, H. 1928. Die Gliederung der Sternopleural-region des Lepidopterenthorax. *Zeits. f. Zool.* 131: 181–254.

Wittig, G. 1955. Untersuchungen am Thorax von *Perla abdominalis* Burm. (Larva und Imago) unter besonderer Berucksichtigung des peripheren Nervensystems und der Sinnesorgane. *Zool. Jahrb. Anat. u. Ontog.* 74(4): 491–570.

Zalokar, M. 1947. Anatomie du Thorax de *Drosophila melanogaster*. *Rev. Suisse de Zool.* 54(2): 17–53.

Sur l'Apparition de Gonoductes hétérologues au cours du Développement des Termites, des Blattes et des Orthoptères

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RÉSUMÉ

Chez les embryons de blattes et de grillons, Heymons (1895) avait observé l'apparition d'ébauches plus ou moins importantes, mais éphémères, de gonoductes hétérologues.

Nous avons découvert des structures comparables chez les jeunes larves de plusieurs espèces de Termitidae: chez le mâle, le canal déférent (qui se termine à la base du 9ème sternite) porte une petite expansion ventrale au niveau du 7ème segment (rudiment d'oviducte); chez la femelle, l'oviducte (qui aboutit à la base du 7ème sternite) présente une ramification analogue mais partant vers l'arrière (rudiment de canal déférent). Ces ébauches sont visibles seulement dans les espèces dont les gonades sont très peu différenciées à l'éclosion.

Chez Gryllus domesticus, *dont les gonades, à la naissance, sont peu évoluées, nous observons des formations identiques, mais chez* Blattella germanica, *où la différenciation des gonades est beaucoup plus avancée, il ne subsiste aucune ébauche hétérologue chez le nouveau-né.*

Il est ainsi suggéré que, primitivement, les embryons d'insectes passent par un stade transitoire d'indifférenciation sexuelle.

Au cours de recherches étendues sur le polymorphisme des termites supérieurs ou Termitidae (Noirot, 1955), nous avons été amené à préciser le développement post-embryonnaire de l'appareil génital d'un grand nombre d'espèces, surtout en ce qui concerne les castes neutres. Au cours de ces recherches, une attention particulière fut donnée aux gonoductes qui, bien souvent, permettent seuls de déterminer le sexe des larves, des ouvriers et des soldats: le canal déférent se termine à la base du 9ème sternite tandis que l'oviducte aboutit à la partie postérieure du 7ème sternite abdominal.

Dans beaucoup d'espèces, nous avons observé, chez les jeunes larves, des structures que nous interprétons comme des vestiges de gonoductes hétérologues, et qui rappellent de façon tout à fait frappante des formations identiques décrites par Heymons (1895) chez les blattes et les Orthoptères. Rappelons tout d'abord les observations du célèbre embryologiste.

Chez les embryons de grillons et de blattes, l'oviducte, chez les femelles, aboutit à la base du 7ème segment, et garde cette position chez l'adulte, tandis que chez les mâles le canal déférent, qui se termine d'abord à la base du 10ème sternite, voit son ouverture passer au cours de l'embryogénèse, à la base du 9ème sternite; à l'éclosion, la position est donc la même que chez les termites, traduisant d'ailleurs une disposition primitive chez les Pterygotes. Mais en outre, Heymons observe que, chez l'embryon de *Gryllus* mâle, le canal déférent porte, au niveau du 7ème segment, un filament ventral aboutissant, à la partie postérieure du 7ème sternite, à une ampoule terminale, ce filament devant donc être homologué à un oviducte. La même disposition s'observe chez les blattes. Dans les stades ultimes de l'embryogénèse, l'ampoule terminale de l'oviducte disparaît chez le mâle, il ne subsiste que la partie proximale, rudimentaire, de l'oviducte. Chez les embryons femelles, Heymons n'observe pas d'ébauche de canal déférent, mais seulement les ampoules terminales à la base du 10ème sternite, ces formations disparaissent d'ailleurs avant l'éclosion.

Ainsi, chez ces insectes, le tractus génital, tout au début de sa différenciation, semble passer par un stade d'indifférence sexuelle, où les ébauches d'oviductes et de canaux déférents coexistent, aussi bien chez les mâles que chez les femelles, à l'image de ce qu'on observe chez les vertébrés (canaux de Wolff et de Müller).

Nos recherches sur les termites sont tout à fait en faveur de cette interprétation. Soulignons tout d'abord que nos observations portent, non pas sur des embryons mais sur des larves. Chez les termites supérieurs (Termitidae) les larves nouveau-nées ont des gonades quasiment indifférenciées, tandis que les gonoductes sont bien formés. Dans beaucoup d'espèces, les vestiges des formations hétérologues sont encore bien visibles, la partie proximale seule étant conservée. D'une façon générale, on observe à peu près au niveau du 7ème segment (juste en arrière de la jonction de la gonade et du gonoducte) la réunion entre les canaux mâles et femelles. Chez le mâle, le reste d'oviducte est un mince filament qui part vers la face ventrale en direction du 7ème sternite, mais ce filament s'amincit très vite et n'aboutit jamais à l'ectoderme ventral. Chez la femelle, le vestige de canal déférent se détache vers l'arrière, dorsalement à l'oviducte; quand il est bien développé, on le voit se recourber vers la face ventrale, en direction des styles (9ème segment) mais là encore le canal hétérologue n'est jamais complet, sa partie postérieure manque toujours. Nous n'avons observé aucune trace d'ampoules terminales hétérologues.

Nous avons trouvé de telles ébauches bisexuées des gonoductes dans des espèces très variées. Dans la famille des Termitidae, ces formations ont été rencontrées dans toutes les sous-familles étudiées, avec une importance très variable d'une espèce à une autre; parmi les espèces où leur développement est maximum, citons: *Nasutitermes maculiventris*, *Syntermes wheeleri*, parmi les Nasutitermitinae; *Microcerotermes fuscotibialis*, chez les Microcerotermitinae; *Termes hospes*, *T. baculi*, *Cubitermes proximatus*, chez les Termitinae; *Bellicositermes natalensis*, *Sphaerotermes sphaerothorax*, *Acanthotermes acanthothorax*, chez les Macrotermitinae.

Dans la plupart des cas, les vestiges du canal hétérologue disparaissent après la première mue, quelquefois seulement après la seconde. Beaucoup plus rarement, ils persistent chez les ouvriers ou les soldats; ainsi, les soldats femelles de *Termes baculi* et les ouvriers femelles de *Cubitermes proximatus* possèdent encore des rudiments très nets du canal embryonnaire mâle.

Il n'est pas possible de mettre en parallèle la persistance plus ou moins longue d'un gonoducte de l'autre sexe avec la position systématique des termites; en revanche ce phénomène paraît lié à la rapidité de développement de la gonade. Ainsi, chez des Termites aussi primitifs que les Calotermitidae (*Calotermes flavicollis*, *Neotermes aburiensis*), les larves, à l'éclosion, ne montrent aucune formation pouvant rappeler une ébauche de l'autre sexe, mais leurs gonades ont déjà atteint un degré de différenciation beaucoup plus marqué que celles des Termitidae du même stade. Il en est de même du reste chez les blattes et les grillons: nous avons étudié les gonoductes chez les larves nouveau-nées de *Gryllus domesticus* et de *Blattella germanica*; dans la première espèce, un vestige de gonoducte hétérologue se retrouve aussi bien chez les mâles que chez les femelles, avec une disposition identique à celle présentée par les termites, tandis que, dans la seconde, aucune trace ne persiste dans aucun des deux sexes; or les gonades de grillons nouveaux-nés sont encore presque indifférenciées, tandis que celles des blattes montrent, à l'éclosion, un état beaucoup plus avancé (chez les femelles, certaines cellules sont déjà en meïose).

Il nous paraît vraisemblable que la différenciation d'une double ébauche des gonoductes est un fait primitif chez les insectes: outre les exemples précédents, signalons que Wheeler (1893) a décrit chez l'Orthoptère *Conocephalus* l'apparition chez l'embryon femelle d'ampoules terminales dans le 10ème segment abdominal, homologues des ampoules mâles; en outre, il faut rappeler le cas du forficule (Heymons 1895), où, dans l'embryon, le canal de la gonade présente deux branches complètes aboutissant respectivement au 7ème et au 10ème segment, la branche antérieure régréssant dans les deux sexes, la branche postérieure devenant l'oviducte chez la femelle, le canal déférent chez le mâle.

Ainsi, primitivement, l'embryon d'insecte passerait par une phase d'indifférenciation sexuelle, comme celui des vertébrés, la première ébauche de la gonade étant identique chez les mâles et les femelles, et les deux types de gonoductes apparaissent simultanément dans tout l'individu. Un tel état est évidemment fugace, et n'apparaît nettement, dans les espèces actuelles, que chez les formes primitives où l'appareil génital se différencie précocement et évolue lentement.

BIBLIOGRAPHIE

Heymons, R. 1895. Die Embryonalentwickelung von Dermapteren und Orthopteren unter besonderer Berücksichtigung der Keimblatterbildung. Gustav Fischer, éditeur. Jena. 136 p.

Noirot, Ch. 1955. Recherches sur le polymorphisme des Termites supérieurs (Termitidae). *Ann. Sci. Nat. Zool.* 17: 399–595.

Wheeler, W. M. 1893. A contribution to insect embryology. *J. Morph.* 8: 1-160.

DISCUSSION

R. Geigy. 1. Considérez-vous les ébauches d'oviductes et de spermiductes qu'on trouve parfois chez les embryons, comme disques imaginaux bloqués? 2. Les corps allates donnent-ils l'impression d'être fonctionnels? 3. Avez-vous observé des cellules neurosécrétrices?

Ch. Noirot. 1. Les ébauches des gonoductes sont des formations mésodermiques apparaissant chez l'embryon; l'ébauche hétérologue semble régresser progressivement d'arrière en avant. 2. Les corps allates des ouvriers de termites paraissent fonctionnels, bien qu'ils soient plus petits que ceux des sexués (beaucoup d'ouvriers sont encore capable de muer). 3. Je n'ai pas étudié la neurosécrétion.

The Musculature of the Black Widow Spider, *Latrodectus mactans* (Fabricius) (Araneae: Theridiidae)

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ABSTRACT

By means of serial section and dissection, five hundred and forty individual muscles were found in the adult female Latrodectus mactans, *and five hundred and thirty-six in the male. The absence of muscles in the male palpal pretarsus represents the only sexual difference found.*

Despite the reduction of the eighteen original segments of the arachnid body to the three somatic regions of spiders, the segmental nature of the musculature is evident, especially in the extrinsic muscles of the cephalothoracic appendages, and in those compressing the abdominal cavity.

The musculature of the Black Widow was found to correspond generally to that described by Brown for Agelena. *The muscles of the endosternite are as described by Millot, those of the basal segments of the cephalothoracic appendages as described by Steinbach, those of the terminal segments of the legs as described by Snodgrass, those of the cheliceral claw as described by Schimkewitsch, those compressing the abdomen as described by Millot, and Rasmont, those of the respiratory book lungs as described by Kästner, those of the genital aperture as described by Purcell, and those of the venom gland as described by Reese. All work mentioned, except that of Reese, was carried out on other species of spiders.*

Among muscles found in the Black Widow spider, but not described in other species, are those of the coxal gland, the colulus, the ampullate silk duct and the midgut, and some of the muscles of the pedicel and the abdomen. The muscles designated "abdominal sac" by various authors are considered to be vestiges of a laterally placed dorso-ventral musculature originally joining tergites and sternites. The nature of the intrinsic musculature of the palpi supports the belief that these appendages represent modified legs.

Homologies are proposed between the muscles of the pedicel and those of the abdominal segments, between the extrinsic muscles of the spinnerets and those of the coxae of the legs, and between the intrinsic muscles of the lateral spinnerets and those acting on the trochanter of the legs.

DISCUSSION

A. SHULOV. Have you seen any changes during ontogeny? 2. Presumably there must be changes in the stages I and II of spiderlings. 3. What muscles exactly take part in the ejaculation of venom?

J. G. REMPEL. 1. The study of the embryology of *L. mactans* has been completed and submitted for publication. The study of the anatomy of the adult is preparatory to a study of the postembryonic development. 2. That is to be expected since the newly emerged spiderling is incapable of movement. 3. The poison glands are provided with muscles that run over the entire length of the gland.

The Postembryonic Development of *Cochlidion limacodes* Hufn. (Lepidoptera: Cochlididae)

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ABSTRACT

Cochlidion limacodes *Hufn. is a small ochre-coloured moth with a wing-length of well over 1 cm. The eggs, about 0.9 mm long and 0.65 mm broad, are laid singly on leaves of forest trees, particularly oak, and the hatching period is from 8–10 days in June–July. The newly-hatched cylindrical larvae are pale green, about 1 mm in length and 0.40 mm in breadth, and on the back and sides they have numerous volcano-shaped warts. Concealed in these is a large pin-shaped hair which is everted by aid of the blood pressure about 20 minutes after hatching, giving the larvae their characteristic "hedgehog-like" appearance. After 7–8 days the first moult occurs; the larvae are now provided instead with shorter spine-shaped hairs. This hair form is retained during the following instars, but after the last (5th) moult these hairs have been replaced by few extremely delicate hairs. The apple-green larva, about 12 mm long, now resembles a tortoise (of.* Limacodes "testudo"*) or a naked snail ("slug-caterpillar"). The reddish brown cocoon, about 8 mm long, is barrel-shaped; the pupa, like that of the Micro-lepidoptera, has free legs and wing-sheaths, and is not formed until late after the wintering.*

INTRODUCTION

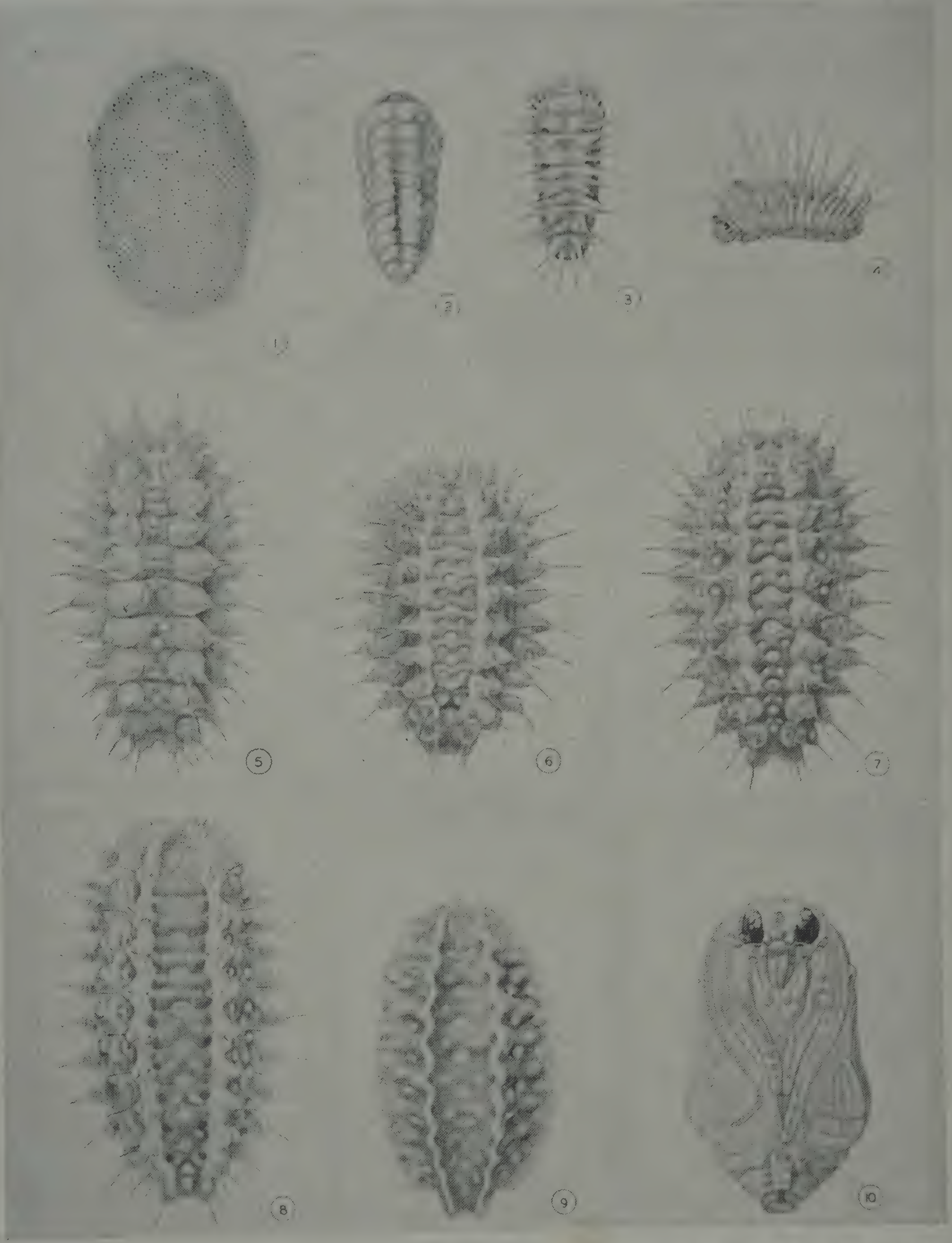
In my studies during a number of years on the embryology of the Lepidoptera (Holst Christensen 1937, 1942, 1943, 1950, 1953 and 1955) it has often been necessary to make extensive rearings in order to procure egg material. These have afforded ample opportunities to make observations on the appearance and behaviour of the larvae employed, during the various stages of the metamorphosis. This applies particularly to the larva of the moth *Cochlidion limacodes* Hufn., on whose embryonic and postembryonic development I have reported in various papers (Holst Christensen 1943, 1950, 1952, 1953 and 1955). In the exposition to follow I shall give an account of the highly interesting postembryonic development of this animal as described in my previous paper (cf. Holst Christensen 1950).

MATERIAL AND METHODS

In Denmark *Cochlidion limacodes* Hufn. is a fairly rare small ochre-coloured moth. The female is a little larger than the male; the wing measure is 1.3 cm and 1 cm respectively. The fore-wings are ornamented with a pair of distinct, blackish-brown transverse bands, and the hind-wings of the male are blackish-brown with a lighter border. In Denmark, and in Europe, the Cochlididae, a primitive family within the Macrolepidoptera, are represented by two genera, viz. *Cochlidion* Hübner and *Heterogenea* Knoch, each with one species, viz. *limacodes* Hufn. and *asella* Schiff. In America, Asia and Africa several hundred species appear to be distributed over more than a hundred genera. *Cochlidion limacodes* occurs mainly in the southern parts of Denmark, and the moth is out in the months of June and July. The female lays the eggs singly on leaves of various forest trees, particularly oak, but in the laboratory I have found that it also readily deposits its eggs on the inner side of the glass containers and cellophane cages in which it is confined, a fact of which I have taken advantage in studying the embryonic development in vivo (cf. Holst Christensen 1953).

THE EGG

The egg (Fig. 1), measuring about 0.90 mm in length and about 0.65 mm in breadth, is flat, scale-like, and oval. It is surrounded by a thin, transparent egg shell, chorion (Ch), which is provided with a characteristic sculpturing (Chs) reminiscent of the meshes of wire netting. At one end of the egg is the micropyle apparatus (Mi), consisting of two concentric circles of wedge-shaped "leaves", the inner of which delimit a centrally placed area with about 6–8 micropyle canals (Mik) intended for the passage of the sperms. According to the temperature the embryonic development takes from 8 to 10 days in June–July.



Figs. 1–10. Immature stages of *Cochlidion limacodes* Hufn., dorsal view except Figs. 1, 4, 10. (After Holst Christensen, 1950, except Fig. 1, 1953). 1, living egg about 1 day old, x 33. Blastoderm stage. Note numerous fatty droplets (F) of which yolk mass consists, as well as peripheral cytoplasmatic layer, the periplasm (Pe), with the conspicuous blastoderm cells (Bl) only partly marked off. (Yz), clear outer zone of egg shell. For other abbreviations see text; 2, newly-hatched larva, x 30; 3, young larva, half an hour old, x 30; 4. young larva, lateral view, half an hour old, x 30; 5, larva after first moult, x 22; 6, larva after second moult, x 15; 7, larva after third moult, x 11; 8, larva after fourth moult, x 10; 9, larva after fifth moult, x 5.5; 10, pupa, ventral view, x 5.5.

THE LARVAL INSTARS

The newly-hatched larva (Fig. 2) is about 1 mm long and about 0.40 mm broad. The form is flat cylindrical and the colour is light-green with a darker green stripe in the middle of the back. Furthermore, on the back, on each side of the middle, is a row of 11 volcano-shaped warts, each provided with a little dark ring on the top. The small brown head is strongly chitinised and as a rule it is not visible from above, because it is drawn in under the prothorax. On this a characteristic cruciform mark is observed.

About 15-20 minutes after hatching the tiny larva is clearly changed (Fig. 3), being now provided with long mobile hairs with a little "side-point". The hairs grow very fast at first, being everted from the above-mentioned warts, probably by the aid of the blood pressure. I have not succeeded in finding a satisfactory explanation of the biological significance of these peculiar pin-shaped larval hairs, which gives the animal its characteristic "hedgehog-like" appearance (Fig. 4).

The tiny *Cochlidion*-larva gnaws off the epidermic layer of the leaves in the small hollow to which it adheres. The gnawing marks shine like silver when the leaf is looked at against the light. When the time for the first ecdysis is approaching no more food is taken, and the larva turns a somewhat paler colour.

After a larval period of 7–8 days the first moult takes place and a green larva emerges (Fig. 5), diverging very much in appearance from an usual caterpillar. The animal which, viewed from above, is elongate oval but plano-convex from the side now measures about 1.88 mm in length and 0.83 mm in breadth. On either side of the median line of the back 11 pairs of cross-grooved warts are found; in front, in addition, one pair of bigger front-warts; on the sides 11 pairs of side-warts are seen, each of which is provided with an awl-shaped, unbranched hair, whereas the back-warts have two such. A dark greenish stripe is observed in the central line of the back and a whitish one below the side-warts. The small brownish head is usually not seen, because it is drawn in under the enormous prothorax, which is provided on the upper side with a bigger sausage-shaped spot and a smaller wing-shaped one.

After a larval time of about 7 days the second ecdysis takes place. The form of the larva (Fig. 6), when seen from above, is now approximately egg-shaped, and the animal seems to be more flat than in the previous instar. It now measures about 2.66 mm in length, about 1.78 mm in breadth, and about 1.44 mm in height. As usual 11 pairs of back-warts and one pair of front-warts are seen, the former each consisting of two small warts. The primary colour of the caterpillar is greenish, and in the median line of the back about 10 whitish spots are observed. The small brownish head is as a rule completely hidden by the enormous prothorax, which is provided on the upper side with a bigger V-shaped spot together with a smaller one.

About 8 days after the second larval instar the third moult takes place. Viewed from above the larva (Fig. 7) is approximately elliptical and it now measures 3.81 x 2.31 x 1.66 mm respectively. The colour is deep green, and in the green median line of the back, 9 rhomboid spots are seen. There are, as usual, 11 pairs of cross-grooved back-warts present, and they are double on the top. The head is light-green, the prothorax, on the other hand, grass-green with 2 V-shaped marks on the top.

About 7 days after the third larval instar, the fourth ecdysis takes place. The larva (Fig. 8), is now approximately elongate oval when seen from above. From the side it superficially resembles a *Chiton*. The measures are 6.21 x 3.57 x 2.43 mm respectively. The middle field, which is provided with 11 whitish rhomboid spots, is of a grass-green colour and is, as usual, flanked by 11 pairs of big greenish back-warts. The prothorax is green and provided in front with a cream-coloured stripe with a reddish spot in the middle, on the top it has 2 comma-shaped spots.

After a larval time of about 8 days in the fifth instar, the fifth moult takes place. The form of the larva (Fig. 9) is now totally changed. Seen from above, the animal is oval, while from the side it is more like a cucumber. At first the colour is yellowish green, later on it becomes more whitish green. The measurements of the larva are now 10.71 x 5.64 x 4.21 mm. On each side of the middle part of the back the somewhat older larva has a yellowish stripe, on the inner border of which are observed 9 cherry-red spots of elongate oval form in a row; furthermore, a yellowish line is seen on the conspicuous side-bulge. The head is greenish and has a distinct conical spinneret, and the prothorax is green and provided with 2 brown rhomboid chitinised thickenings on the upper side. The underside of the larva is sea-green and the thorax bears 3 pairs of small conical legs. Instead of "pro-legs" the animal has, on either side of the abdomen, 8 big secondary sucker discs.

Already after the first ecdysis the appetite of the larvae increases very much and in each of the following instars it grows steadily. After the third and fourth ecdyses the larvae are more commonly found at the border of the leaves where big holes bear witness to their activity. When feeding here they take up a characteristic riding attitude, and the taking of food goes on completely hidden under the enormous collar-shaped prothorax.

THE COCOON

When the larva has reached a size of 12.5 x 7.5 x 4.5 mm respectively, no more food is taken. The animal, which now resembles a tortoise (cp. *Limacodes "testudo"*) or a naked snail ("slug-caterpillar") seeks out a suitable place between two leaves lying near each other. Between these the larva spins a red-brown, barrel-shaped cocoon which is about 8½ mm long and about 5½ mm broad. At the time of the leaf-fall the cocoon falls to the ground, and the wintering takes place in the larval stage.

THE PUPA

The oval pupa (Fig. 10), which measures about 7¾ mm in length and about 4½ mm in breadth, does not appear until late in the new year. At first the chrysalis is light-green, later greyish. The eyes are coal-black, the colour of the face light-brown, the mouth parts, on the other hand, dark-brown. The antennae are many-jointed, stout and brownish. The grey legs and wing-sheaths are free, just as in the Microlepidoptera, and the brownish abdominal segments are provided at the top with a border of small, rust-coloured, bristle-shaped chitin hairs.

Of the imago there exist so many good descriptions and figures in the literature that I have not considered it expedient to proceed to that topic here.

REFERENCES

Christensen, P. J. Holst. 1937. Zur Histologie und Embryologie der überwinterten Eier von *Orgyia antiqua* Linné. *Zool. Jb. Anat.* 62: 567–582.

Christensen, P. J. Holst. 1942. Embryologische und zytologische Studien über die erste und frühe Eientwicklung bei *Orgyia antiqua* Linné (Fam. Lymantriidae, Lepidoptera). *Vidensk. Medd. fra Dansk naturh. Foren.* 106: 1–223.

Christensen, P. J. Holst. 1943. Serosa-und Amnionbildung der Lepidopteren. *Entom. Medd.* 23 (Jubilæumsbind): 204–223.

Christensen, P. J. Holst. 1950. Studien über die postembryonale Entwicklung bei *Cochlidion limacodes* Hufn. (Fam. Cochlididae, Lepidoptera). *Det Kgl. Danske Vidensk. Selskab, Biol. Skrift.* 7: 1–36.

Christensen, P. J. Holst. 1952. The development in vivo of time-fixed eggs of *Cochlidion limacodes* Hufn. (Fam. Cochlididae, Lepidoptera). *Trans. Ninth Int. Congr. Entom.* 1: 219–222.

Christensen, P. J. Holst. 1953. The embryonic development of *Cochlidion limacodes* Hufn. (Fam. Cochlididae, Lepidoptera). A study on living dated eggs. *Det Kgl. Danske Vidensk. Selskab, Biol. Skrift.* 6: 1–46.

Christensen, P. J. Holst. 1955. Om Bygningen og Udviklingen af Haarene hos den nyklækkede Larve af *Cochlidion limacodes* Hufn. *Norsk Entom. Tidsskr.* 9: 137–139.

The Gastral Digestive Organs in the Male Carpenter Ant, *Camponotus pennsylvanicus* DeGeer, Prior to and at Swarming

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ABSTRACT[1]

The digestive organs in the gaster of C. pennsylvanicus *males consist of the crop, the proventriculus or gizzard, the ventriculus or midgut, the intestine with attached Malpighian tubules, the rectum and the anus which opens on the eighth gastral segment dorsal to the genitalia. The anatomy and histology of the gastral digestive organs are described for males taken from nests during the month of May and for those captured when they were swarming for the nuptial flight in July.*

The arrangement of the organs and their histology are similar to that which has already been described for the Camponotus *workers. In the male ventriculus, however, the epithelial cells are taller and their shapes somewhat different from those in the worker. There is food in all the gastral digestive organs. Most males dissected had 18 Malpighian tubules, some had 20, and one had 23; in this latter case, one was branched.*

In the swarming males most of the gastral digestive organs are collapsed or reduced in diameter. The crop, proventriculus, and ventriculus are practically lying on the floor of the first three gastral segments; this condition leaves large spaces in the dorsal, anterior end of the gaster. The system is empty of food. Histologically, only the epithelial cells of the ventriculus in these swarming males show marked changes. These ventricular epithelial cells are degenerating, and the lumen of this organ is filled with basophilic-staining granules.

DISCUSSION

P. J. HOLST CHRISTENSEN. It seems to me to be very interesting that you have demonstrated that the fat body in the male carpenter ant is completely used up after swarming. The Danish physiologist, T. Weis-Fogh, has shown that the Desert Locust, *Schistocera gregaria* (Forshal) uses up fat during the migratory flight. Don't you think that it is fairly probable that the army ant does the same when swarming?

JAMES FORBES. At swarming all the fat body is not consumed, but all material in the digestive tract is, and the organs of this system are collapsed. My opinion is this decreases the body weight of the male for the nuptial flight.

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[1] For complete text see "Observations on the gastral digestive tract in the male carpenter ant, *Camponotus pennsylvanicus* DeGeer (Formicidae, Hymenoptera)" in *Insectes Sociaux* 3: 505–511 (1956).

Pigmentation in the Thoracic Musculature of Cockroaches and Related Orthoptera and the Analysis of Flight and Stridulation

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ABSTRACT

Although many species of cockroaches fly, the action of the pterothoracic musculature is not fully understood. In Periplaneta americana, *in which the males fly but the females do not, the musculature of both sexes is the same anatomically. Freshly killed, unfixed individuals reveal a conspicuous difference. The adult male pterothoracic musculature is opaque and pigmented pink; that of females is hyaline and white. Newly moulted adult males have hyaline, white muscles, but show a gradual postmetamorphic development of pigmentation. This sexual variation in muscle pigmentation is also found in* P. fuliginosa, P. brunnea, P. australasiae, Parcoblatta pennsylvanica, P. virginica, *and* Supella supellectilium.

In adult Leucophaea maderae, Blaberus craniifer, B. giganteus, Blatella vaga *and* Pycnoscelus surinamensis *the pterothoracic musculature is pink pigmented in both sexes.*

In Nauphoeta cinerea, Blatta orientalis, Neostylopyga rhombifolia, Blattella germanica, Eurycotis floridana *and* Cryptocercus punctulatus, *the pterothoracic musculature is hyaline white in both sexes. In all species examined there exists a correlation between wing reduction and hyaline white musculature. In* Diploptera dytiscoides *with shortened tegmina and long, folded hindwings, the mesothoracic musculature is hyaline white, and the metathoracic musculature is pink pigmented in both sexes.*

In four species of Gryllids, the pigmentation of the musculature in the mesothorax is specifically confined to the stridulating muscles of male crickets. In the metathorax, species with short or vestigial hindwings have a hyaline white musculature, whereas long-winged flying forms have a pink pigmented musculature.

The relationship of pigmentation to metabolism and the flight mechanism is discussed.

INTRODUCTION

Many paths of approach to an understanding of the flight mechanism in insects have been taken. These include the role of the exoskeleton, the mechanical action and physiological properties of the flight musculature, the action of the nervous system, and the aerodynamics of flight. Numerous investigators have explored these methods with considerable success, so that we now have a useful storehouse of knowledge pertaining to insect flight as recently summarized by Chadwick (1953). Since we lack a satisfactory phylogenetic series of insects leading to the perfection of various flight mechanisms as evidenced in modern flying forms, we are still far from understanding how the specific elements of the flight mechanisms as we know them today have been gradually integrated in the course of this evolution.

Cockroaches appear, at first glance, a poor group of insects for contributing to our understanding of the evolution of flight. Very little is known concerning the flying abilities of the various species, and those which do fly are relatively poor flyers when compared with numerous species of Hymenoptera and Diptera. Sotavalta (1947) has shown that *Ectobius lapponicus* has a wingbeat frequency of 44/sec. and males of the cockroach *Periplaneta americana* have a wingbeat frequency of 32–36/sec., in contrast with many species of aculeate Hymenoptera with frequencies ranging from 90–277/sec. and most Diptera with frequencies ranging from 100–1000/sec. Although many species of cockroaches have lost the ability to fly, the appearance of non-flying forms independently among many genera is of particular interest. In the absence of an adequate phylogenetic series of insects in which flight has evolved, what can be learned from the comparative study of a group of insects in which the regression or secondary loss of the ability to fly has frequently taken place?

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[1] John Simon Guggenheim Memorial Fellow, (U.S.A.) 1955.

[2] Present address: Marine Biological Laboratory, Woods Hole, Mass.

THE PTEROTHORACIC MUSCULATURE OF COCKROACHES

Although many species of winged cockroaches can fly, the action of the pterothoracic musculature is not fully understood. Snodgrass (1952) has already called attention to the difficulty in understanding how the cockroach is able to fly at all. In many insects, the tergal movements which indirectly produce the vibration of the wings are in large part effected by the dorsoventral, tergosternal muscles and the dorsal longitudinal, intertergal muscles. This type of flight is undoubtedly a highly evolved one but its mechanism of functioning is relatively simple. In the cockroach *Periplaneta americana*, the tergosternal muscles that are partly responsible for the upstroke in other insects are entirely absent, and the dorsal longitudinal muscles (Fig. 1, Dl), usually required for the downstroke, are very weak. Further, the wing-bearing nota of the cockroach are connected by intervening membranes, so that the normal contracting action of the dorsal longitudinal muscles which results in arching the tergum in other insects would here probably be expended in merely pulling the nota together.

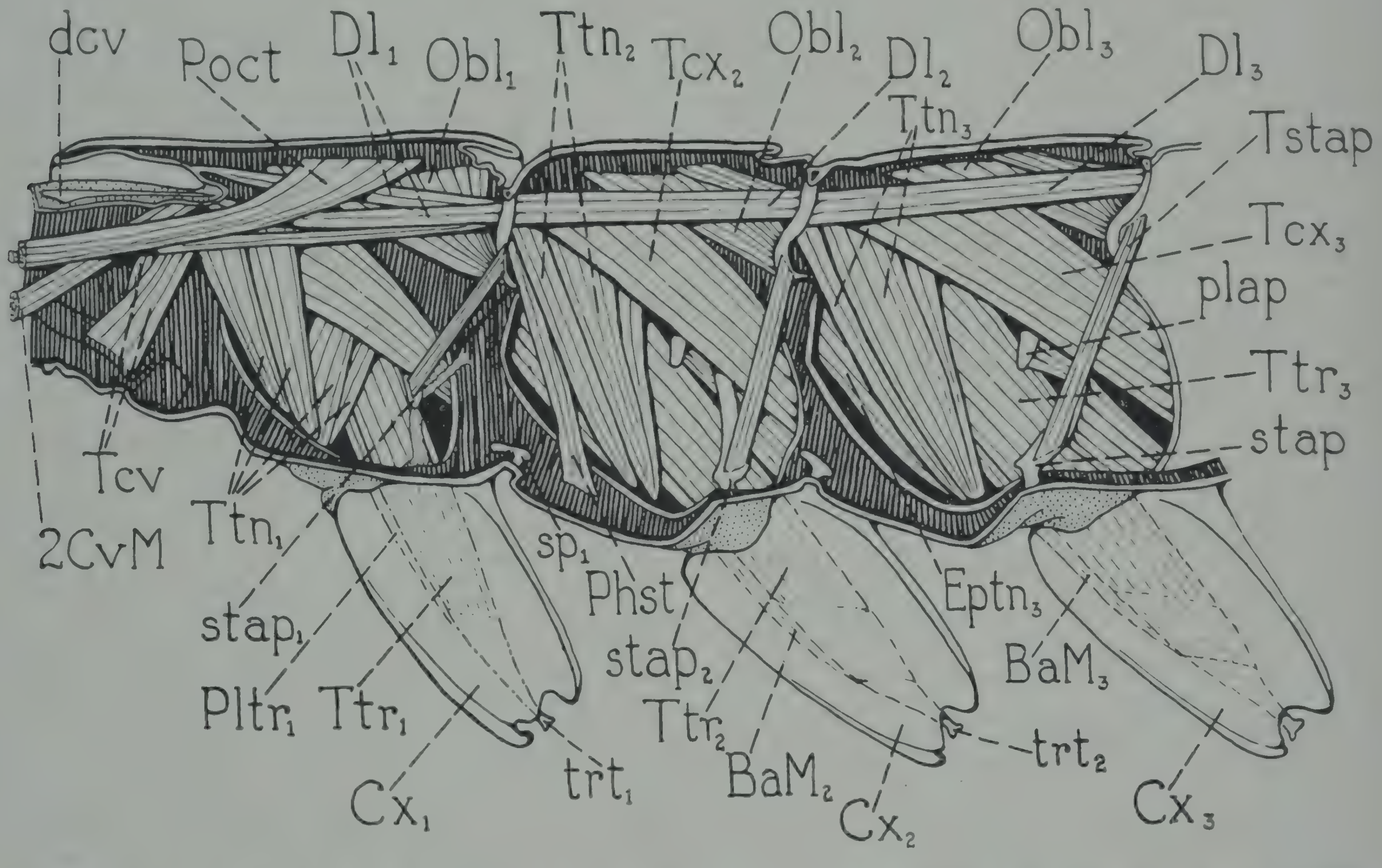

Fig. 1. Mesal view of right half of thorax of *Periplaneta americana*, with ventral longitudinal muscles dissected away. BaM, basalar muscle; 2CvM, second cervical muscle to head; Cx, coxa; dcv, dorsal cervical sclerite; Dl, dorsal longitudinal muscle; Eptn, Episterno-trochantinal muscle; Obl, oblique tergal muscle; Phst, phragmal muscle of the basisternum; plap, pleural apodeme; Pltr, pleuro-trochanteral muscle; Poct, postoccipital muscle to pronotum; sp, spinisternal apodeme; stap, sternal apodeme; Tcx, tergocoxal muscle; Tcv, laterocervical muscle from pronotum; trt, trochanteral tendon; Tstap, muscle from sternal apodeme to succeeding tergum; Ttn, tergotrochantinal muscle; Ttr, tergotrochanteral muscle.

The dorsal longitudinal muscles, however, do not seem to be essential for flight. Levereault (1938) has already shown that in the mantis, *Stagmomantis carolina*, in which the musculature is similar to that of the cockroach the dorsal thoracic longitudinal muscles are absent in both the winged segments. Nevertheless, if not a rapid flyer, the mantis is a capable one. Likewise Fuller (1924) has shown that dorsal longitudinal muscles are absent in winged, flying termites.

The thoracic musculature of the cockroach *Periplaneta americana* has been studied in detail anatomically by Carbonell (1947). The large size of the basalar and subalar muscles in both winged segments of the cockroach led him to conclude that they must play an important role in flight. The basalar and subalar muscles are also two of the largest muscles in the winged segments of the cockroach *Leucophaea maderae*. Since the subalar sclerite is intimately connected with the second and third axillary sclerites of the wing, (see Fig. 2) Snodgrass considered that the subalar muscle may possibly exert a depressor action on the wing. Chadwick (1953) has suggested that in insects in which the dorsal longitudinal muscles are poorly developed or absent the depression of the wing may be caused directly by shortening of both the basalar and subalar muscles alone. In view of the size and position of these two muscles, it is not unlikely that such an action contributes to the depression of the wing in cockroaches.

Which muscles are involved in the elevation of the wings? The tergosternal muscles, which normally help to depress the notum which in turn results in the upstroke of the wings, are absent in both the winged segments of the cockroach *Periplaneta americana*. Instead both these segments have a number of so-called "leg muscles" which originate on the notum and are inserted on the trochantin, the rim of the coxa, and the trochanteral apodeme, which could, provided the leg base were held rigidly, depress the notum and elevate the wings.

DIFFERENCES IN FLIGHT BEHAVIOUR OF MALE AND FEMALE PERIPLANETA

If we accept this tentative indication of the mechanics of the pterothoracic musculature in the flight of *P. americana* we still face an enigma. Males of this species are good flyers, to the extent that cockroaches fly, whereas females are not. According to Rehn (1945) both sexes of *Periplaneta* species fly in tropical and subtropical regions[3], but in north temperate climates the females appear to have lost this ability. According to Mallis (1954), six adult female *P. americana* thrown into the air at 82°F fluttered their wings but failed to fly. I have obtained similar results with laboratory-reared American cockroaches in both the northern United States (New York and Wisconsin) as well as in Germany. The same appears to be true for laboratory-reared *P. fuliginosa*. At 71°F *fuliginosa* males were thrown into the air in the evening. On the first two trials the first male flew, but lost altitude rapidly. On four successive trials this male maintained his altitude and continued in a horizontal direction until a wall or window was reached. This was repeated with a second male with the same general results—the second male flew more successfully, sometimes partly circling around in flight, after the first two trials. Apparently at this temperature, as in many other insects, a short warm-up period is required. Trials under the same conditions with females gave the following results. On the first trial the female fluttered her wings weakly but fell straight down. On eight successive trials she came down without wing fluttering. The same result was obtained with a second female. Additional investigation along these lines remains to be done, but these preliminary experiments do demonstrate the difference in the flight behaviour of males and females of these species of *Periplaneta*.

PIGMENTATION DIFFERENCES IN THE THORACIC MUSCLES OF COCKROACHES

If an examination of the pterothoracic musculature of *P. americana* is made using preserved specimens, no significant anatomical difference in the muscles of the two sexes can be found to account for this difference in flying ability. When freshly killed cockroaches are dissected without the use of fixing fluids or Ringer's solution, however, a conspicuous difference in the colour of the pterothoracic muscles of the two sexes is visible. In both the meso- and metathorax of the male, the larger muscles are opaque and pigmented pink, whereas the corresponding muscles of the female are hyaline and white. In contrast, the prothoracic muscles of both sexes are hyaline and white.

The muscles which are pigmented pink in both winged segments of the male are listed in approximate decreasing size (Carbonell's numbers in parentheses) and are as follows:

1.	(135c; 177c)	Basalar muscle from upper margin of episternum to lower part of trochanteral apodeme (Fig. 3, BaM)
2.	(135a; 177a)	Tergo-trochanteral muscles (Fig. 1, Ttr)
3.	(118, 119, 120; 161, 162, 163)	Tergo-trochantinal muscles (Ttn)
4.	(128; 169)	Subalar muscles (SaM)

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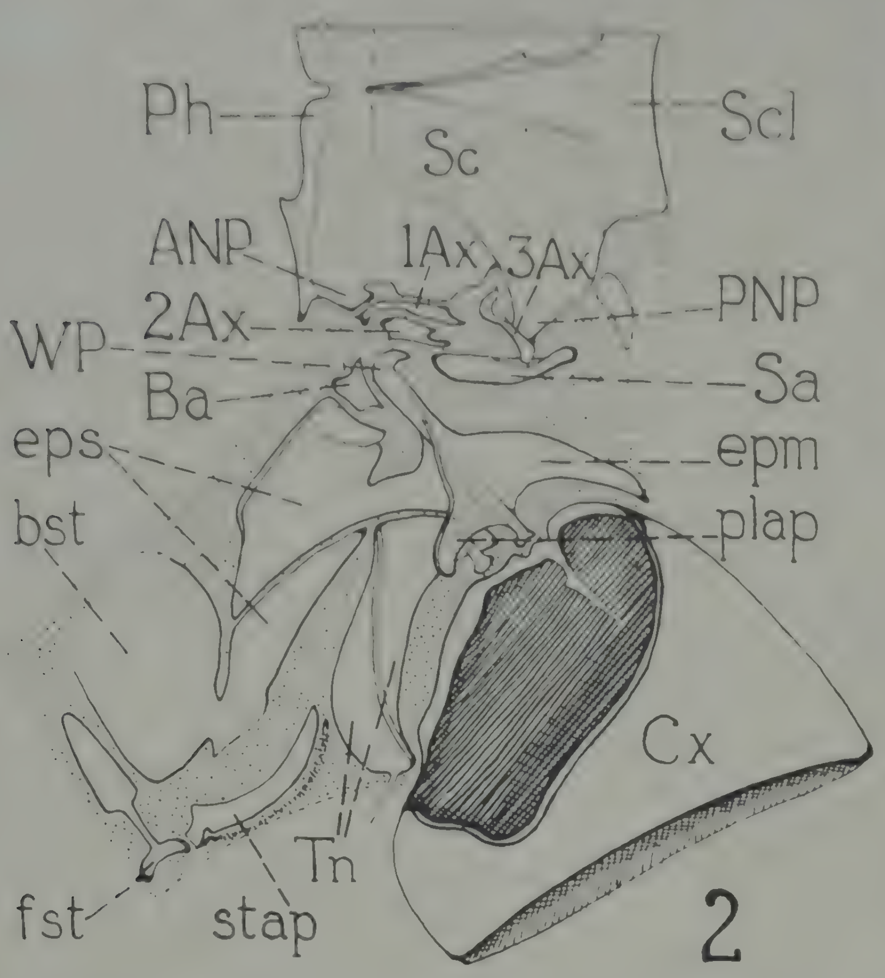
[3] Rehn, who observed *P. americana*, *P. australasiae* and *P. fuliginosa* in flight, assumed that both sexes flew, but did not confirm this by examination of flying individuals (correspondence, 1956).



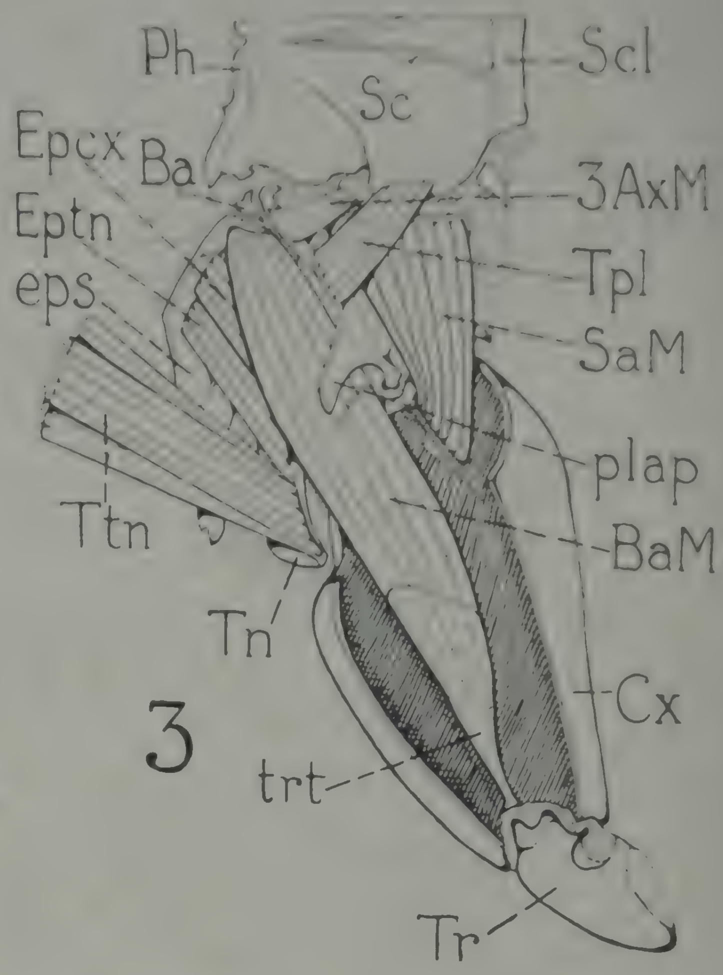


Fig. 2. Sclerogram of metathoracic segment, *P. americana*, internal view.

Fig. 3. Additional pigmented muscles of metathorax, *P. americana*. ANP, anterior notal wing process; 1Ax, 2Ax, 3Ax, first, second and third axillary sclerites; AxM, pleural muscle to third axillary; Ba, basalare; BaM, basalar muscle; Epcx, episterno-coxal muscle; epm, epimeron; eps, episternum; Eptn, episterno-trochantinal muscle; Fst, Furcasternite; Ph, phragma; PNP, posterior notal wing process; Sa, subalare; SaM, subalar sclerite; Sc, scutum; Scl, scutellum; Tn, trochantin; Tpl, tergopleural muscle; WP, pleural wing process. For other abbrevations see Fig. 1.

5. (129, 130, 131; 174, 175, 176)	Tergo-coxal muscles to posterior coxa (Tcx)
6. (112, 113; 155a, 155b)	Oblique tergal muscles (Obl)
7. (126; 167)	Episterno-coxal muscle to anterior coxa (Epcx)
8. (122, 123, 124; 164, 165, 166)	Episterno-trochantinal muscles (Eptn)
9. (114)	Tergo-pleural muscle (Tp1)

Males and females of *Leucophaea maderae* have been observed to fly distances of 10–12 feet spontaneously in an insectary and the flight ability of both sexes can be confirmed by flight trials such as described for *P. americana* and *P. fuliginosa*. Examination of the thoracic muscles of *Leucophaea maderae* indicates that both males and females possess a pink pigmented pterothoracic musculature corresponding to the pink pigmented muscles of male *P. americana*. The prothoracic muscles are likewise hyaline white in both sexes.

The metabolic significance of the pink pigmented muscles has been revealed by a number of biochemical studies. Barron and Tahmisian (1948) found that the oxygen consumption of pterothoracic muscle from male *P. americana* is double that of females. Sacktor and Bodenstein (1952) showed that cytochrome *c* oxidase activity of male *P. americana* is significantly higher than in the female. Harvey and Beck (1953) found that succinoxidase activity of thoracic muscle from the male American roach is three times that of the female. McShan, Kramer and Schlegel (1954) were able to confirm the higher succinoxidase activity of pink pigmented muscles of male *P. americana* as compared with the corresponding hyaline white muscles of females, and in addition were able to demonstrate that in *L. maderae*, in which both males and females have pink pigmented pterothoracic muscles, succinoxidase activity is approximately the same in both sexes. On the other hand ATP-ase activity, which is approximately equivalent in the pterothoracic muscles of male and female *L. maderae*, is higher in the white pterothoracic muscles of female *P. americana* than in the comparable pink muscles of the male (McShan, Kramer and Olson, 1955). These studies suggested that in adult cockroaches there exist two metabolically distinct types of pterothoracic muscles—a relatively more active pink pigmented musculature and a hyaline white musculature of lesser activity.

With this in mind a comparative study of the thoracic muscle pigmentation of 19 species of cockroaches was undertaken. These studies will be described in detail in a separate publication, but the general results may be summarized here. In a number of species of cockroaches a sexual variation in adult pterothoracic musculature was found such as occurs in *Periplaneta americana*—i.e., the male adult musculature is pigmented pink, whereas that of the female is hyaline white. This condition prevails in *P. fuliginosa*, *P. australasiae*, *P. brunnea*, *Parcoblatta virginicus*, *P. pennsylvanica* and *Supella supellectilium*. Another group is comparable to the condition found in *L. maderae* in which the adults of both sexes have a pink pigmented pterothoracic musculature. These include *Blaberus gigantea*, *B. craniifer*, *Pycnoscelus surinamensis* and *Blattella vaga*. There is still a third group in which the pterothoracic musculature of the adults of both sexes is hyaline and white. These include *Nauphoeta cinerea*, *Eurycotis floridana*, *Neostylopyga rhombifolia*, *Cryptocercus punctulatus*, *Blatta orientalis* and *Blattella germanica*.

In those adult cockroaches above in which a pink pigmented musculature is present, the muscles of both the mesothorax and metathorax are equally pigmented. An exception to this condition occurs in the beetle roach *Diploptera dytiscoides*, which derives its common name from the fact that the reduced tegmina resemble the elytra of a beetle. Folded underneath the reduced tegmina are a pair of long hind wings. In this cockroach the mesothoracic muscles of both sexes are hyaline white, but the metathorax, bearing the long hind wings in both sexes, contains pigmented muscles.

All the above roaches with a pink pigmented pterothoracic musculature as adults, possess a corresponding hyaline white musculature in their last nymphal stage. Newly moulted adult male *P. americana* have a hyaline white musculature, but show a gradual postmetamorphic development of pigmentation during the first 72 hours of adult age. A similar postmetamorphic development of muscle pigmentation takes place in both sexes of adult *L. maderae*, although some slight pigmentation may actually begin prior to metamorphosis in this species.[4]

MUSCLE PIGMENTATION, WING LENGTH AND THE ABILITY TO FLY

In those adults in which a hyaline white pterothoracic musculature is present there is a greater or lesser reduction of the tegmina and wings. Although there is sometimes an equal reduction in wing length in both males and females of a species, as in *Nauphoeta cinerea*, in which both sexes have brachypterous tegmina and wings, the reduction in wing length generally appears first in females. A doubtful group in this regard are the females of species belonging to the genus *Periplaneta*, but comparison measurements of *P. americana* and *P. fuliginosa* indicate that the tegmina and wings of the female are shorter than those of the male in these species. In no species of cockroach that I know does the male have shorter wings than the female.

The three native species of the genus *Ectobius* in Great Britain clearly depict the evolutionary trend of female wing reduction. In all three species the tegmina and wings of the male are fully developed. In *E. pallidus* those of the female are also fully developed, but in *E. lapponicus* the tegmina of the female are about two thirds the length of the abdomen and the wings are reduced. Finally, in *E. panzeri* the tegmina of the female are just a little longer than wide and the wings are much reduced. *Parcoblatta* is another genus in which the males have long wings and are strong flyers, whereas the females of different species show various degrees of reduction of the tegmina and wings.

Species of cockroaches possessing a hyaline white musculature as adults lack the ability to fly. Apart from apterous species, such as *Cryptocercus punctulatus* and those with vestigial tegmina, such as Eurycotis *floridana* and *Neostylopyga rhombifolia*, brachypterous forms such as the males of *Blatta orientalis* and both sexes of *Nauphoeta cinerea* are non-flying. Females of the genus *Periplaneta* with a relatively small reduction in tegmina and wing length are likewise non-flying. The question arises as to whether the initial regression towards flightlessness is determined by the reduction in wing length or the presence of a hyaline white musculature of low metabolic activity.

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[4] Colonies of P. *americana* may show some variation in the onset of pigmentation. Protocols (1950-53) of laboratory colonies of P. *americana* in Wisconsin indicate that newly moulted male adults always showed a hyaline white pterothoracic musculature upon dissection. In Germany, however, the pterothoracic musculature of newly moulted male *P. americana* adults is semi-opaque and shows a light pink tinge. Last instar male nymphs examined shortly before they are about to moult show a hyaline pterothoracic musculature but are also lightly pink tinged. Male last instar nymphs examined during the early or mid-instar show a hyaline white pterothoracic musculature. The determining factors in this somewhat earlier onset of pigmentation remain to be investigated.

Sotavalta (1947, 1952) has indicated that there tends to be a constant flight ratio in insects dependent on the body weight of the insect, the wing-inertia, the wingbeat frequency and the wing stroke amplitude. In general increased body weight or a reduction in wing inertia is compensated for by an increased wingbeat frequency (or increased stroke amplitude). Actual wing mutilation experiments with a variety of insects have shown that when varying proportions of the wing are cut away, the wingbeat frequency rises proportionally. Thus, we might postulate on theoretical grounds that even with a reduction in wing length, females could still fly if their muscles were able to produce an adequate wingbeat frequency.

According to Sotavalta (1954), however, male *P. americana* show no change of frequency when the wing inertia is altered, and therefor the size of the wings might well become the determining, mechanically limiting factor in the loss of flight. Male *P. americana* have a tegmina length which averages 28.8 mm, compared to the average of 21.9 mm for females. If we select the occasional non-gravid females with a tegmina length of 24.0-24.5 mm, however, we find that their flight behaviour differs little from what has been previously indicated. These uniformly flutter their wings on the first or second trial, when thrown into the air, and come almost straight down. Thereafter, on successive trials they plummet down with either no wing fluttering, or with occasional wing tremors. On the other hand, if we take a male with a tegmina length of 31.0 mm and cut these tegmina and underlying hind wings down to 25.0 mm, he flies quite well on six flight trials, always reaching a wall or window, rather than dropping to the floor. When the tegmina and wings are further cut down to 22.0 mm, the male still flies fairly well, although he drops almost to within 2-3 feet of the floor, before achieving a horizontal flight. When the tegmina and wings are cut below 20.0 mm, flight is no longer possible and the male drops to the floor. Even after 20 trials, however, the males continue to flutter their wings actively and attempt to fly. In contrast the females hardly make more than one or two actual wing fluttering attempts. In *P. fuliginosa* the average tegmina length of males and females are even more closely approximated—24.7 mm for males, 21.6 mm for females. Thus the loss of flight in female *Periplaneta* appears to be primarily dependent on the presence of a musculature which is metabolically incapable of the necessary flight-sustaining function.

An important objection still remains to considering the pink pigmented muscles specifically those involved in producing the wingbeat of the cockroach. Cockroaches, as is well known, are very swift runners, and seem to prefer to make use of their legs rather than their wings. Might these active muscles which are frequently termed "leg muscles" not be required for their running behaviour rather than flight? The answer derived from the above comparative study is decisively negative. Species with hyaline white muscles as adults are also swift runners—i.e. *Blattella germanica*, *Blatta orientalis*, *Neostylopyga rhombifolia* and *Eurycotis floridana*. As has already been mentioned, pigmented species as adults have a hyaline white musculature in their nymphal instars, and these nymphs run as swiftly as their pink pigmented adults. The postmetamorphic developement of a pigmented musculature, therefore, seems specifically correlated with the flight function of the adult.

Surprisingly few changes in the origins and insertions of the muscles are sufficient to modify the pterothoracic segments of the nymphs for the adult flight function. On the other hand flight requires a musculature with properties of contraction and endurance distinct from those of the leg muscles. Since these muscles are practically the same in flying as in non-flying forms, those who term them "leg muscles" are not wrong. The same muscles which are involved in running in the nymphs are converted into flight muscles in the adult by a change in their physiological properties. Tiegs (1955) recently called attention to the functional and histological plasticity of the flight muscle in insects and pointed out that changes in the physiological properties of the flight muscle of orthopteroid species are attended by changes in the histology of its fibres. These *postmetamorphic* changes in muscle pigmentation should be added to the premetamorphic changes in muscle fiber histology. The development of a flight musculature from the leg musculature suggests that the evolution of flight itself may have been dependent in part on the gradual physiological and histological changes of an existing, well-developed and complex leg musculature such as is found in cockroaches. Subsequent changes appear to have been in the direction of a mechanically simpler, but metabolically more active musculature.

MUSCLE PIGMENTATION AND WING LENGTH IN CRICKETS

In cockroaches we are confronted with a group of insects in which variation in flight behaviour, together with correlated differences in muscle pigmentation and wing length, occurs either as a sexual dimorphism within a species, or as an interspecific difference. A possible exception to this, as we have noted, may be the females of species belonging to the genus *Periplaneta*. It would be interesting to know whether the muscles of tropical flying female *P. americana* are pigmented, and on what factors such variation within the species may be dependent.

To test whether or not the correlation between wing length and pigmentation extends to other groups of orthopteroid insects we may turn to Gryllidae. Among crickets wing length is an extremely variable character. There occur not only interspecific differences and sexual dimorphism, but variations of a given sex within a species. In particular such variations have been recorded in species of the genera *Acheta*, *Nemobius* and *Anaxipha*. According to Fulton (correspondence 1956) some species are always macropterous, others are always brachypterous; some are dimorphic for wing length, while others display several intermediate stages in the loss of functional wings. The studies of Sellier (1954) dealing with the phenomenon of wing polymorphism have indicated similar types of variability for ten species of crickets belonging to several genera distributed in Europe, North Africa and Asia.

In North America, I have examined the thoracic musculature of the common field cricket, *Acheta assimilis*. Several hundred specimens collected in New York State in various localities showed fairly uniform characteristics as regards wing length. The tegmina in both sexes, although showing some slight variability, were all brachypterous, and the hind wings were vestigial. In the females, all muscles in the pro-, meso-and metathoracic segments were hyaline white, and the male exhibited a similar hyaline white musculature with the exception of a few dorsoventral muscles in the mesothorax which were somewhat opaque and pigmented yellow. Among these specimens, however, there was a single female with long hind wings extending beyond the abdomen to the posterior tip of the cerci. In this form the dorsal longitudinal and dorsoventral muscles of the metathorax were pigmented an orange-pink colour and were opaque; the muscles of the pro- and mesothorax were translucent and white. DuPorte (1920) in his paper on the musculature of *Acheta assimilis* (as *Gryllus assimilis*) called attention to the strong development of the dorsal longitudinal muscles in the metathorax of long-winged females, and Sellier (1947) pointed out the regularity with which occasional macropterous forms occur among brachypterous species of Orthoptera.

Among a large number of *Nemobius fasciatus* collected in two or three localities (all from similar habitat—open grassland near a stone wall, Taconic State Park, N.Y.), a single macropterous female was collected in an otherwise vestigial-winged population. The distribution of muscle pigmentation was the same as indicated in *A. assimilis* above. The pro-, meso- and metathoracic muscles of the normal vestigial-winged females were all hyaline white; those of the males, with the exception of three pigmented muscles in the mesothorax, were also hyaline white. The single long-winged female showed hyaline white pro- and mesothoracic muscles, but the dorsal longitudinal and dorsoventral muscles of the metathorax were opaque and pigmented yellow.

The common house cricket, *Acheta domesticus*, is a long-winged species, in which the hind wings in both sexes extend to or just beyond the cerci. In the female, the muscles of the pro- and mesothorax are all hyaline white, but five dorsoventral muscles, as well as the dorsal longitudinals, in the metathorax are opaque and pigmented pink. The same distribution of hyaline and pigmented muscles is found in the male, with the exception that three dorsoventral muscles in the mesothorax are pigmented pink. Both sexes are flyers. In the laboratory, approximately 2–3 weeks after becoming adults, these insects displayed a characteristic type of behaviour. From about eight o'clock in the evening until after midnight the adults kept vibrating their hind wings while standing in place. This they continued for one or two minutes, then ran about very excitedly. On approaching an inverted flower pot or other object they climbed to the top, moved about excitedly in different directions, then selected one and jumped. If the jump carried the insect over the aquarium wall, the jump merged into flight. If not, the wing vibration, excited running about and jump was repeated after a short interval. These crickets flew quite well, and only stopped when they encountered a wall or other obstacle. This wing vibration and flight behaviour was repeated on various evenings over a period of several weeks.

The long-winged *Gryllus bimaculatus* shows a distribution of pigmented muscles similar to that encountered in *A. domesticus.*

MUSCLE PIGMENTATION AND STRIDULATION IN MALE CRICKETS

Apart from the fact that long-winged crickets show a characteristic metathoracic muscle pigmentation, we find that in the mesothorax of the males of all four species above, three muscles are pigmented a flesh-pink or yellow colour. These include two muscles originating on the tergum and inserted on the trochantin and posterior margin of the coxa, (Fig. 4, Tcx_2, Ttn_2) and the tergo-trochanteral muscle (Ttr_2). In the mesothorax of the female of all four species the muscles are always hyaline and white. The pigmented mesothoracic muscles of crickets sometimes show a more yellowish tinge than the pink-pigmented pterothoracic muscles of cockroaches, and the significance of that colour difference has yet to be clarified. Nevertheless from what we have seen of the relation of pigmented muscles, high metabolic activity and flying ability in cockroaches it seems reasonable to conclude that these pigmented muscles of the mesothorax are responsible for the movement of the tegmina, or stridulation of the males.

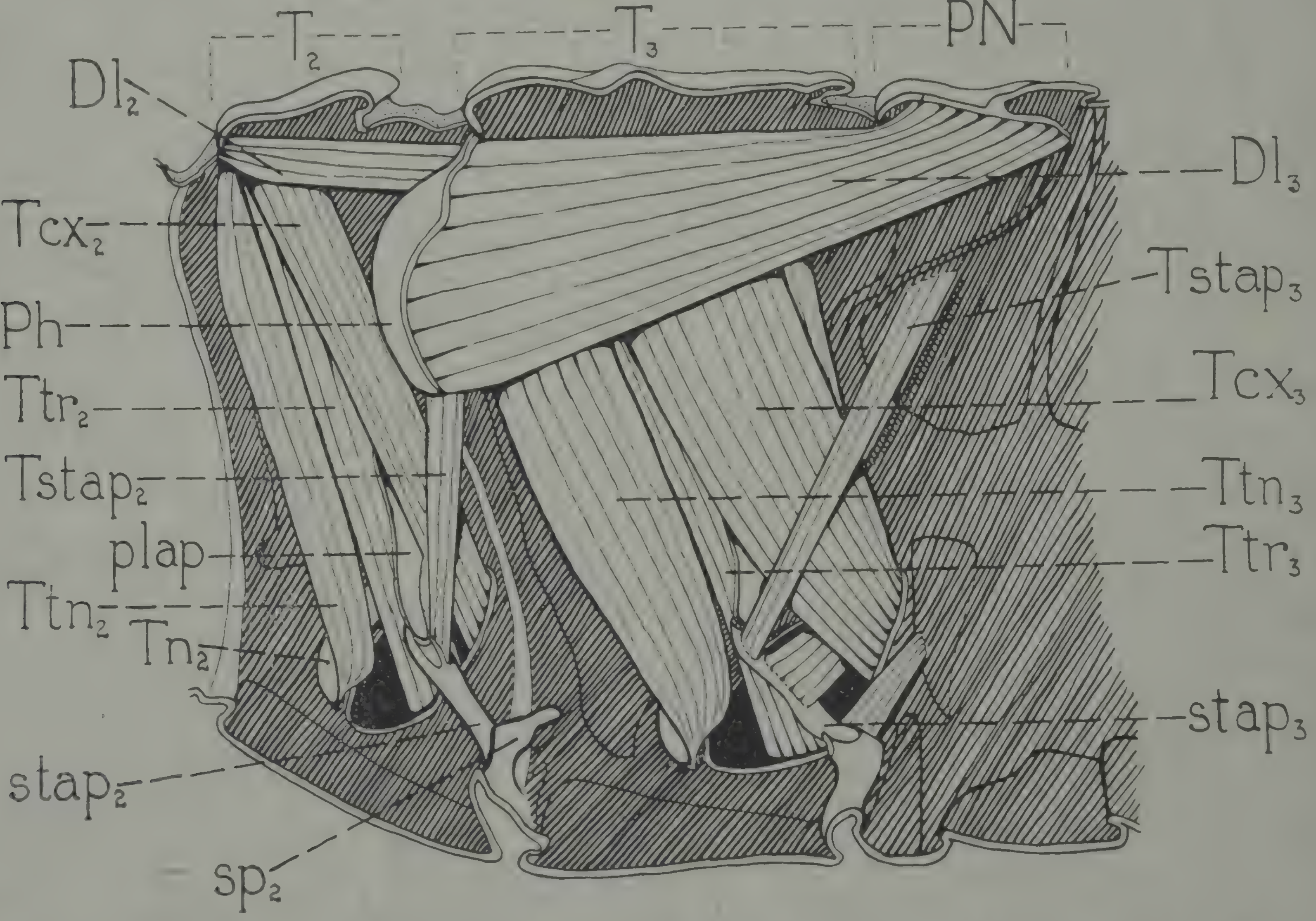

Fig. 4. Mesal view of right half of pterothorax of the common house cricket, *Acheta domestica*, with ventral longitudinal muscles dissected away. In the mesothorax of the male the tergo-trochantinal muscle (Ttn_2), the middle branch of the tergo-trochanteral muscle (Ttr_2) and the tergo-coxal muscle (Tcx_2) are pigmented. In the metathorax the dorsal longitudinal (Dl_3), the tergo-trochantinal (Ttn_3), the tergo-trochanteral (Ttn_2), and the tergo-coxal (Tcx_3) muscles are pigmented, as well as the subalar and episterno-coxal muscles, not shown. PN postnotum; T, tergum.

GENERAL DISCUSSION

The preliminary results of these studies are as follows:

(1) Species of cockroaches which fly have a pink pigmented opaque pterothoracic musculature as adults, whereas the corresponding musculature of their nymphal instars is hyaline and white.

(2) In many genera of cockroaches there has been an independent regression or secondary loss of flying ability which is correlated with the absence of muscle pigmentation in the pterothorax and the reduction in the length of the tegmina and wings.

(3) In crickets a similar correlation between the loss of flight, the absence of muscle pigmentation and the reduction of wing length is found within polymorphic forms within the species as well as in species of separate genera.

(4) Stridulation in male crickets is correlated with the presence of pigmented muscles in the mesothoracic segment.

(5) For anatomical purposes pigmented thoracic muscles appear to be a valuable aid in determining those muscles which are responsible for the production of an effective wingbeat and stridulation.

Although we are dealing with a secondary loss of flying ability in cockroaches with its attendant loss of muscle pigmentation, it is evident that a similar development from non-pigmented to pigmented muscles has taken place in the evolution of flight itself. Ontogenetically this change from a hyaline white musculature to a pigmented musculature of higher metabolic activity takes place primarily as a *postmetamorphic* change. This is evident in the adult males of several species of *Periplaneta* as well as in both sexes of adult *L. maderae*.

The colour terms "hyaline white" and "opaque pink", used in surveying the extent of pigment variation in the flight muscles of different species of cockroaches, have only a limited value. Barron and Tahmisian (1948) have shown by the use of spectrophotometric analysis that there is more than twice as much cytochrome *c* in the flight muscle of male *P. americana* as in the female muscle, and Sacktor *et al.* (1953) have suggested that the colour differences in the muscles of the two sexes may be due to differences in cytochrome content. Preliminary quantitative microspectroscopic analysis of the flight muscles of this cockroach do indeed confirm that there is approximately twice as much cytochrome *c* present in the pink-pigmented flight muscles of adult males as compared with those of adult females (Kramer and Shappirio; unpubl. data). However, there is a certain darkening of the muscle of males which takes place during the first three days of adult life which does not seem to be correlated with any significant change in cytochrome *c* content, and this requires further investigation.

The red and white muscles of vertebrates, where the colour is apparently due to myoglobin, provide an interesting comparison. Lawrie (1952) has demonstrated that in general the red muscle of various vertebrates (high in myoglobin content) is associated with high enzymatic activity for succinic dehydrogenase, succinoxidase and cytochrome oxidase. ATPase activity, on the other hand, is higher in white muscle (low in myoglobin). Although no myoglobin has been demonstrated in the muscles of cockroaches their pink and white flight muscles show an association of relative succinoxidase and ATPase activity parallel to those of vertebrates (see above).

These physiological variations of the musculature within the species as well as between species may throw some light on a number of problems in behaviour. Newly moulted adult male *P. fuliginosa* 24–48 hours old show flight behaviour comparable that of old adult females—i.e. they may flutter their wings actively and attempt to fly on successive trials but they lose altitude and drop almost straight down, or they flutter their wings and attempt to fly only on the first trial or two, then come straight down with very weak wing fluttering on successive trials. Bronson (1943) has mentioned the fact that male field crickets are not accomplished singers when they first become adults but seem to require a few days of practice before their singing is perfected. Since a similar increase in the pigmentation of the flight and stridulatory muscles takes place in Gryllidae, it is not unlikely that, aside from the hardening of the cuticle, the improvement of singing ability may be dependent in part on the postmetamorphic physiological maturation of the musculature.

The fact that changes in behaviour are intimately correlated with changes in the physiological properties and histological structure of the musculature has been demonstrated in the recent study of Levenbook and Williams (1956) on the flight musculature of Diptera. In *Phormia* there is a gradual increase in cytochrome *c* during the first week of adult life, which remains at a relatively constant level thereafter. As the cytochrome *c* increases there is a corresponding increase in the size of the sarcosomes of the muscle. Finally, wingbeat frequency gradually increases over the first week and then also approaches a constant. Williams and Chadwick (Chadwick 1953, p. 593) have shown a similar increase of wingbeat frequency during the first few days of adult life in *Drosophila*. It is of interest that wingbeat frequency of male *Drosophila* at any given age is greater than that of females. Whatever role nervous and endocrine factors may play in regulating the physiological state of the muscles, it is apparent that at any given time the state of that musculature plays a considerable role in the responses of the insect.

Apart from the modification of the ordinary hyaline white musculature into a pigmented musculature with physiological properties capable of sustaining flight as evidenced in cockroaches and other Orthoptera, there has been an additional muscular adaptation to flight in insects. The thoracic muscles of the cockroach *P. americana* are of the "synchronous" type—i.e. a single electrical stimulus to the motor nerve evokes a single contraction of the muscle. The highly specialised indirect flight muscles of Hymenoptera, Diptera and Coleoptera, as well as the tymbal muscles of cicadas, are of the asynchronous type, (Roeder, 1951; Pringle, 1954) and are somewhat different physiologically. In these latter an initial arrival of nerve impulses apparently induces a state of excitation and resulting tension in the muscle without immediately causing contraction. Thereafter (during steady flight) nerve impulses occur at a much lower frequency than the wingbeat and are not synchronized with the contractions of the indirect flight muscles. The potentialities of this asynchronous muscle system has been revealed by Sotavalta (1953). Male specimens of a species of *Forcipomyia* (Ceratopogonidae) have a flight musculature which may normally produce over a thousand complete cycles of contraction and relaxation per second. Under experimental conditions a wingbeat frequency of 2,218/sec. has been obtained in a specimen of *Forcipomyia* with wings cut and exposed to high temperature.

Although these muscle systems are often designated as distinct types (hyaline white leg muscles, pigmented synchronous and asynchronous flight muscle etc.), the recent comparative studies of Tiegs (1955) suggest that they are but convenient descriptive terms in the *gradual* evolution of the flight musculature throughout the orders of insects. The variation and changes in the pterothoracic musculature of isolated genera of cockroaches and crickets, correlated with the functions of flight, lend support to this concept. Although comparative methodology provides us with important insight into what nature is actually doing, additional experimental study is necessary for a fuller understanding of such phenomena. Nevertheless, the union of studies in comparative morphology with comparative behaviour (ethology) may be expected to furnish a valuable area of investigation.

REFERENCES

Barron, E. S. G., and T. N. Tahmisian. 1948. The metabolism of cockroach muscle, *Periplaneta americana*. *J. Cell. Comp. Physiol.* 32: 57–76.

Bronson, W. S. 1943. The grasshopper book. *Harcourt, Brace and Co.*, New York.

Carbonell, C. S. 1947. The thoracic muscles of the cockroach *Periplaneta americana (L.)*. *Smith. Misc. Coll.* 107: 1–23.

Chadwick, L. E. 1953. Chapters 22–24. *In* Insect physiology, ed. by K. D. Roeder.

Crampton, G. C. 1927. The thoracic sclerites and wing bases of the roach *Periplaneta americana* and the basal structure of the wings of insects. *Psyche* 34: 59–72.

DuPorte, E. M. 1920. The muscular system of *Gryllus assimilis* Fabr. *Ann. Ent. Soc. Amer.* 13: 16–52.

Fuller, C. 1924. The thorax and abdomen of winged termites. With special reference to the sclerites and muscles of the thorax. *Union S. Africa, Dept. Agric. Ent. Mem.* No. 2: 47–78.

Harvey, G. T., and S. D. Beck. 1953. Muscle succinoxidase in the American cockroach. *J. Biol. Chem.* 201: 965–973.

Lawrie, R. A. 1952. Biochemical differences between red and white muscle. *Nature* 170: 122–123.

Levenbook, L., and C. M. Williams. 1956. Mitochondria in the flight muscles of insects. III. Mitochondrial cytochrome *c* in relation to the aging and wingbeat frequency of flies. *J. Gen. Physiol.* 38(4): 497–512.

Levereault, P. 1938. Morphology of the Carolina mantis. *Bull. Univ. Kansas* 39 (11): 577–633.

Mallis, A. 1954. A handbook of pest control. 2nd ed. *MacNair Dorland*, New York.

Matsuda, R. 1956. The comparative morphology of the thorax of two species of insects. *Microent.* 21(1): 1–65.

McShan, W. H., S. Kramer and V. Schlegel. 1954. Oxidative enzymes in the thoracic muscles of the woodroach *Leucophaea maderae*. *Biol. Bull.* 106(3): 341–352.

McShan, W. H., S. Kramer and N. F. Olson. 1955. Adenosinetriphosphatase activity of American cockroach and woodroach muscles. *Biol. Bull.* 108(1): 45–53.

Pringle, J. W. S. 1954. The mechanism of the myogenic rhythm of certain insect striated muscles. *J. Physiol.* 124(2): 269–291.

Rehn, J. A. G. 1945. Man's uninvited fellow traveller—the cockroach. *Sci. Monthly* 61(4): 265–276.

Roeder, K. D. 1951. Movements of the thorax and potential changes in the thoracic muscles of insects during flight. *Biol. Bull.* 100: 95–106.

Sacktor, B., and D. Bodenstein. 1952. Cytochrome *c* oxidase activity of various tissues of the American cockroach *Periplaneta americana (L.). J. Cell. Comp. Physiol.* 40(1): 1–4.

Sacktor, B., G. M. Thomas, J. C. Moser and D. I. Bloch. 1953. Dephosphorylation of adenosine triphosphate by tissues of the American cockroach, *Periplaneta americana (L.). Biol. Bull.* 105: 166–173.

Sellier, R. 1947. Le polymorphisme alaire chez les Orthopteroides. *Bull. Soc. Sc. Bretagne* 22: 95–112.

Sellier, R. 1954. Recherches sur la morphogenese et le polymorphisme alaires chez les Orthopteres Gryllides. *Ann. Sc. Nat. Zool.* 16: 597–739.

Sotavalta, O. 1947. The flight tone (wing-stroke frequency) in insects. *Acta Ent. Fennica* no. 4: 117 pp.

Sotavalta, O. 1952. The essential factor regulating the wing-stroke frequency of insects in wing mutilation and loading experiments at subatmospheric pressure. *Ann. Zool. Soc. "Vanamo"* 15(2): 1–67.

Sotavalta, O. 1953. Recordings of high wing-stroke and thoracic vibration frequency in some midges. *Biol. Bull.* 104(3): 439–444.

Sotavalta, O. 1954. The effect of wing inertia on the wing-stroke frequency of moths, dragonflies and cockroach *Ann. Ent. Fennici* 20(3): 93–101.

Snodgrass, R. E. 1927. Morphology and mechanism of the insect thorax. *Smith. Misc. Coll.* 80(1): 108 pp.

Snodgrass, R. E. 1952. Arthopod anatomy. *Comstock Publ. Assoc.*, Ithaca, N.Y.

Tiegs, O. W. 1955. The flight muscles of insects—their anatomy and histology—with some observation on the structures of striated muscles in general. *Phil. Trans. R. Soc. London* 656: 221–359.

Sur les Principes d'une Codification de la Terminologie Anatomique et Morphologique Relative aux Insectes

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RÉSUMÉ[1]

L'auteur, à la suite d'une récente expérience lexicographique[2], *pense que les défauts de la terminologie anatomo-morphologique des insectes (néologismes, synonymes, homonymes, noms trop longs, désuets, etc. . . .) justifient un effort de simplification et d'uniformisation.*

Il repousse, pour y parvenir, aussi bien l'argument d'autorité que le vocabulaire-type (tels les nomina anatomica *existant pour les Vertébrés) ou même les Règles strictes (telles celles de la Nomenclature Zoologique). Il propose simplement un ensemble de principes, respectueux des priorités, mais aussi des usages, et soucieux d'universalité, autant que du respect des valeurs nationales.*

Ces principes invalident les noms désuets ou trop longs et les nomina nuda; *ils indiquent les procédures pour le choix du nom de référence de chaque structure et pour sa traduction au moyen des homonymes et synonymes en usage, la création de néologismes, même de traduction, devant être, le plus possible, évitée.*

Ces principes sont tels qu'à chaque structure s'appliquerait un groupe de quatre noms au plus (en allemand, anglais, français, latin, dont le nom de référence) et, éventuellement leurs homonymes en diverses langues; ces noms n'appartiendraient qu'à cette structure et toutes celles identiques ne porteraient que cet ensemble de noms, suffisamment consacré par l'usage pour être aisément acceptable par tous.

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[2] Dupuis, Claude. 1955. Les genitalia des Hemiptères Hetéroptères: Revue de la morphologie; lexique de la nomenclature; Index bibliographique analytique. *Mem. de Mus. Nat. Hist. Nat., n.s.* A: *Zoologie*, 6(4): 183–278.

Morphologically Meaningful vs. Descriptive Terminologies for Use by Taxonomists, with Comments on Interordinal Homologies of Male Genitalia[1]

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ABSTRACT

For many structures (e.g., legs), homologies of major parts among insect orders were obvious from the beginning and taxonomists have almost always used morphologically meaningful names for parts. For other structures, differences in ideas on homologies are still strong and many taxonomists use descriptive terms without regard for homologies. Contrary to some views, the author believes that the advantages of a uniform and morphologically meaningful terminology for taxonomists are great. The dangers of prematurely accepting such a terminology to replace the special descriptive terminologies that have arisen independently in many orders and families are considered, using examples drawn from insect genitalia.

One of the great problems in entomology is to provide for the development and establishment of a terminology for morphological structures. The function of any such terminology is simple: to provide a system whereby entomologists can tell what other entomologists are talking about. In practice, however, it is rare to find two people in complete agreement on how this should be done, and as entomologists tend to be independent in their ways of thinking, there have been proposed a variety of different systems within each insect group.

A major divergence of opinion has occurred in regard to the degree to which homologies of structures among families and orders should be allowed to influence terminology. Where homologies have long been known, and are clear to every observer, it is usual to use a single terminology for all insects. Thus the leg segments of all insect orders receive the same names from all entomologists.

Where homologies are less obvious, descriptive or special systems of terminology for various orders, families, and even genera, have often evolved. Certain taxonomists advocate such special systems because, once established, it is usually perfectly clear what term is to be used for a certain structure and there is no need to change terms as homologies are clarified. One does not have to consider homologies, relationships between groups, or any other basic problems of entomology; one simply follows a system of terms, and is not disturbed if a word is used for non-homologous structures in different families or orders. Because of the use of the same term for unrelated structures in related groups, and for various other reasons, these special systems, or morphologically meaningless systems, do not make it easier for entomologists to understand one another, and often, indeed, lead to confusion.

At the opposite extreme are taxonomists who accept, as soon as possible, terms which are presumed to be morphologically meaningful, i.e., terms which indicate homologies of structures among the various groups of insects. Although it is denied by some, such morphologically meaningful terminologies have evident advantages, I believe, to taxonomic entomologists. Advantages that may be cited for such terminologies are as follows:

A. They increase the ease with which a taxonomist can transfer his interest from one group of insects to another. This is important from the standpoint of developing a body of broadly interested taxonomists instead of narrow specialists.

B. They tend to force or at least encourage specialists to consider developments in entomology in general, not merely in their own narrow field of taxonomic interest.

C. They decrease the necessity for a person studying two or more unrelated groups to learn different names for structures in the two groups.

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[1] Contribution number 943 from the Department of Entomology, University of Kansas, Lawrence.

I feel that it is obvious that the establishment of a more or less uniform terminology for wing veins and cells for all orders, following along the lines advocated by Comstock and Needham, has been an advantage for systematic entomology. That this is so seems to be indicated by the widespread acceptance of this system by systematists working in various insect orders.

From the systematists' viewpoint, the ideal terminology would be one which does not change. Lack of necessity for change, except as the needs of the taxonomists vary, is the principal advantage of the special or descriptive terminologies. The necessity for change, as morphological interpretations vary, is the principal disadvantage of morphologically meaningful terminologies. The question, then, is how can one devise terminologies that will unite the best features of the two systems? Clearly, it would be desirable that homologies and other considerations of morphology be determined with considerable certainty before an established, even though special, system is discarded for a new one based on morphological evidence. Perhaps the most satisfactory way to explain in greater detail some of the problems which arise is to discuss some matters relating to the genital appendages of insects.

In the female, the ovipositor is said, in the standard morphological works, to be made up of appendages of the eighth and ninth abdominal segments. The parts are as follows:

first valvifer	coxite 8
first valvula	gonapophysis 8
second valvifer	coxite 9
second valvula	gonapophysis 9
third valvula	

In the first column are indicated terms applicable to the ovipositor; in the second, the presumed homologies with structures of other segments are indicated. Fortunately, it is possible to homologize the ovipositor parts more or less satisfactorily among such diverse orders as Thysanura, Odonata, and Hymenoptera, so that one set of terms serves for all orders. The fact that Matsuda (1957), supported by ontogenetic data from various earlier authors, believes that the valvifers and valvulae are probably of sternal rather than appendicular origin need not modify the terms in the first column. These terms therefore remain useful for morphologists and taxonomists regardless of the ultimate origin of the structures. This seems to be a desirable arrangement; if the homologies suggested by Matsuda are correct, it would have been an error to discard names such as "valvifer" for the more general term "coxite". I believe *in theory* that it would be better to use names showing the broadest homologies possible (in this case, "coxite", in the middle ear, "hyomandibular" instead of the mammalian "stapes" and the reptilian "columella"). In actual practice, however, it is not necessary, as the example of the ovipositor illustrates, for either morphologist or taxonomist always to use names having the broadest possible application (e.g., coxite); sometimes it is better, for the sake of stability and usefulness, to apply names in a narrower sense. The narrowing should be done, however, not according to taxonomic groupings but according to the probable accuracy of homologies. Since homologies between the ovipositor parts and the parts of a walking leg are not certain, it is best to retain special names such as valvifer, and valvula for the ovipositor.

The situation in regard to male genitalia is far more complicated, partially because of the difficulty of homologizing the various parts. There are two general views as to the relations of male genitalia among insect orders. (1) That they are homologous structures of probably appendicular origin, and (2) that in some orders they are derived from the primary phallic lobes and are not of appendicular origin. It seems to me that it is possible to homologize the structures among the various orders (see Michener, 1944; Gustafson, 1950), for the similarities are evident; to me it seems highly improbable that two-segmented claspers, penis valves, and penis would arise independently in various orders. That such a complicated skeleto-muscular mechanism could arise (e.g., in Hymenoptera) from the membranous phallus and arrive at a condition in which its various parts can apparently be homologized one by one with genitalic parts of other orders in which a similar mechanism is said to be of periphallic origin is most unlikely. Moreover, in the Thysanura certainly, and in Pterygota probably, one can homologize male genitalia with female ovipositor parts.

In view of the enormous morphological diversity of male genitalia, and resultant doubts as to homologies of genitalic parts, it is no surprise that a multitude of terminologies has arisen for these structures. However, in many cases the multiplicity of terminologies has been utterly unnecessary and highly confusing. For example, in the Hymenoptera, the word paramere has been used by one author or another for virtually every paired structure of the male genitalia, and the same word has even been used in other orders for male structures on other segments. There is no need for such careless usage. Snodgrass (1941) and others have shown that there is no difficulty in homologizing male genitalic parts throughout the Hymenoptera, only the genus *Apis*, out of the entire order, presenting major difficulties. Snodgrass, therefore, established a single terminology for the male genitalic parts of the order. As he apparently considered the genitalia of Hymenoptera to lack detailed homologies in other orders, he was not concerned with establishing such homologies, or an interordinal system of terminology.

For reasons indicated above, I believe that the genitalia of Hymenoptera can be homologized with those of other orders. In 1944, therefore, I set up a terminology indicating these relationships using, for example, the word "gonocoxite" to show the relationships with the equivalent structure (second valvifer) of the female ovipositor. I believe that theoretically this was a proper procedure. Yet today it must be admitted that the interordinal homologies among males are not certainly established and that the male-female homologies are also uncertain in Pterygota. Moreover, as already indicated, the valvifers (and hence male "gonocoxites" if the homologies suggested in 1944 are correct) may not be coxal in origin, but are perhaps sternal. It is obvious under these circumstances that parts of the 1944 terminology were, for taxonomists' purposes, premature and that a relatively noncommittal terminology (comparable to valvifer and valvula of the female ovipositor) would be preferable to terms such as gonocoxite and gonostylus. Basal and apical segment of the clasper would have been more appropriate. As the interordinal homologies become more certain, such a terminology can be expanded among the Pterygota. Meanwhile, special terminologies for the male genitalic parts of various orders can be retained by taxonomists as long as serious doubt exists about the interordinal homologies.

We may summarize these ideas by saying that for both the taxonomist and the morphologist, I believe that terminologies should have the following characteristics: (1) usefulness over a wide range of systematic categories (This means a high degree of morphological meaningfulness, or in other words, that homologous structures should have the same names in different systematic groups.), and (2) a high degree of stability. Because of doubtful homologies and changes in ideas as to homologies, (1) and (2) are often in conflict. As descriptive terminologies for structures occurring in special groups are eliminated in favor of morphologically meaningful terminologies of broad application, there is danger of instability resulting from uncertain homologies between groups, between sexes, or between segments of the body. It is recommended that morphologically noncommittal terms of broad application (e.g., valvifer and first segment of clasper) be established in preference to terms of even broader significance (e.g., gonocoxite) based on questionable homologies.

REFERENCES

Matsuda, R. 1957. The comparative morphology of the abdomen of two species of insects. (In press).

Michener, C. D. 1944. A comparative study of the appendages of the eighth and ninth abdominal segments of insects. *Ann. Ent. Soc. Amer.* 37: 336–351.

Gustafson, J. F. 1950. The origin and evolution of the genitalia of the Insecta. *Microentomology* 15: 35–67.

Snodgrass, R. E. 1941. The male genitalia of Hymenoptera. *Smithsonian Misc. Collections* 99(14): 1–86.

DISCUSSION

G. F. Ferris. The trouble with terminology is that we know the morphology of perhaps less than 500 species. There are about 10 million species. Obviously it is too early to establish a fixed general terminology.

G. Steyskal. The Comstock-Needham wing vein terminology is still open to serious question in some places, e.g., median field of Diptera; all veins in Hymenoptera, etc. Veins in reduced venation in C.-N. terminology have cumbersome names for a total of only a few veins.

J. SMART. The desire for priority for morphological terms perhaps comes from workers without close acquaintance with more than one order of Insects.

C. D. MICHENER. I agree with these comments and in no way wished to suggest a priority system for morphological terminology.

The Comparative Morphology of the Male Genitalia of Muscoid Diptera[1]

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Ottawa, Ont.

ABSTRACT

A study was made of the genitalic structure of the higher muscoid flies, and further evidence was found to support Crampton's conclusion that the hypopygium had been rotated through 360° and partially inverted under the abdomen with a consequent crowding of the sterna of the posterior segments.

A search through the Brachycera for a form comparable to the generalized pterygote genitalic form as worked out in other insect orders resulted in the acceptance of the Bombyliid genus Villa *as such a form. Because of the great gap between the Orthorrhaphous and Cyclorrhaphous Brachycera, there was considerable difficulty in tracing the modifications that contribute to muscoid structure, but important details were found in the Scenopinidae, Cyrtidae, and among the Aschiza.*

From this study, it is concluded that the hypopygium consists essentially of the ninth segment with minor elements of the tenth and eleventh segments. The ninth tergum makes up the main capsule, a pair of musculated fragments forming the surstyli. The ninth sternum is lost or incorporated into the gonocoxites which form the main ventral plate and the pregonites, the postgonites being homologous to the gonostyli. The penis valves are incorporated into the penis forming the lateral sclerotized plates.

These findings are discussed in relation to the main views of Zumpt and Heinz, Hennig, and Crampton.

The male genitalia of Diptera, so far as accurate homologies are concerned, have been virtually unknown until recent years. Then, with the work of Crampton in the United States and Hennig in Europe, some order became evident in the confusion. The realization that the structures were homologous with those of other insect orders, and consisted of the same main elements i.e.–ninth segment, gonocoxopodites, penis valves and aedeagus laid the way for final clarification. But there is still a great divergence of opinion as to the identity of these prime elements in the higher families of Diptera, as witness papers by Zumpt and Heinz (1949, 1950), Crampton (1923, 1938, 1952) and Hennig (1936). The work on which I wish to report now is an attempt to further clarify the situation and bring together these divergent opinions.

An important fact to understand is that the terminal abdominal segments—ninth and beyond—have undergone a rotation of 360° and returned to their original position, finally becoming partially inverted under the abdomen. The evidence for this has gradually accumulated until the theory has been generally accepted by workers in the Cyclorrhapha. However, this evidence has not been conclusive, due to the following difficulties.

First, the clockwise rotation of the segments beyond the fifth clearly shown by sclerite displacement in most Aschiza and some Schizophora, and discussed in detail by Crampton, is not apparent in many families, due to a re-establishment of symmetry by fusion and reduction. Secondly, the path of the ejaculatory duct from a ventral position dorsally over the rectum, then ventrally again to connect with the aedeagus, could possibly be due to a migration of the testes which lie free in the body cavity.

In a search for conclusive evidence, two other structures, the tracheal trunks and the abdominal nerves were studied. It proved practically impossible to trace the main tracheal trunks between the spiracles of the postabdomen—fifth to seventh. But in nervous system dissections, it was found that in the Anthomyiids the nerves to the postabdomen follow the same looping path over the digestive tract as does the ejaculatory duct. This evidence can scarcely be explained away.

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[2] Assistant Entomologist.

A study of the pupae of *Musca* and *Drosophila* in an attempt to establish the time of rotation showed that the rotation takes place prior to sclerite formation, indicating that the process is deeply rooted in the Muscoids.

The sclerites of the seventh and eighth segments are strongly displaced and modified by this rotation, the seventh having twisted clockwise through 90° to a lateral position, and the eighth through 180° until its sternum lies dorsally. The terga of the segments are reduced, or, as in many muscoids, absent. The sterna frequently fuse into a synsternum, commonly called the pregenital segment. The sixth segment is at most slightly asymmetrical, and may be either free or fused into the synsternum.

Thus having accounted for the anterior segments of the postabdomen, whose sterna have been considered by Hennig and others to form part or all of the ventral elments of the genital segment, we are free to discuss in detail the composition of the hypopygium itself, and the identity of the prime elements mentioned above.

It will be useful to study first these basic elements as visible in simple Brachycerous form in the Bombyliid genus *Villa*. The ninth tergum is a large broad plate with the anus hidden beneath its posterior margin, surrounded by only faint traces of the 10th and 11th segments. In the ninth segment (as seen in Fig. 1, from a dorsal view with the ninth tergum removed), the gonocoxites are large broad elements with a small apical gonostylus. The ninth sternum is a small plate between the bases of the gonocoxites, and the aedeagus arises from it. The penis valves originate at the base of the gonocoxites and fuse over and around the aedeagus at their tips. But this relatively easily interpreted structure is far removed from the complex structure of the Muscoid hypopygium.

Here there are two main contradictory interpretations. In one school, along with Crampton and Zumpt and Heinz, are those who believe the dorsal element to be strictly tergal—ninth or tenth with the eleventh as a minor element. The claspers, which lie on the lateral margins of this sclerite, are considered then as surstyli or paraboli, secondary extensions of the ninth tergum or tenth sternum respectively, depending on the author.

In the other school, with Hennig, are those who think that a large part of the dorsal element is composed of the gonocoxites fused in with the tergal elements, the claspers then being homologous with gonostyli.

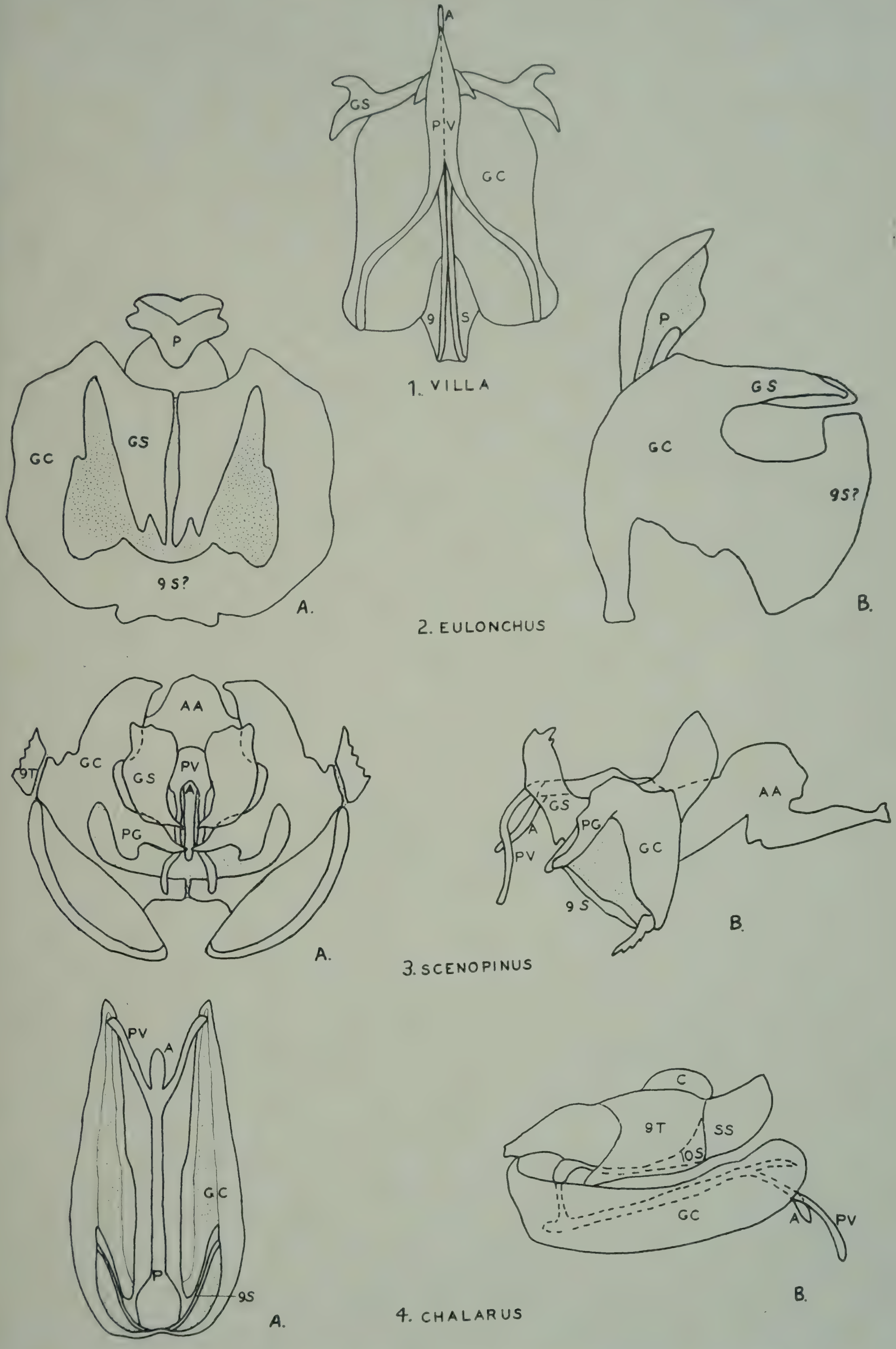
Evidence has been advanced to support one school or the other, but as a rule, this evidence comes from a study of these highly specialized forms and a study of lower Brachycera and Nematocera, rather than from a chain of intermediate forms. Unfortunately this gap is very difficult to bridge since primitive forms directly ancestral to the Cyclorrhapha seem to have completely disappeared.

Studies during 1954 and 1955 led me to believe the explanation of Muscoid structure lay in the Dolichopodidae, where there is an analogous inversion of the postabdomen, with the formation of a true coxotergum. In the examination of Pipunculid genitalia, which I thought to have a primitive form, a similar structure was found. With the knowledge that the claspers of the hypopygium are distinctly and even strongly musculated, data with which Crampton was not familiar, coupled with my aversion to accepting his hypothesis that these claspers arise more or less "de novo", I was almost fully convinced that the "coxotergum" hypothesis was fully valid.

This year, in an attempt to obtain further evidence to conclusively prove this, I found instead strongly contradictory data, which forced me to accept Crampton's surstylus hypothesis. In the most primitive genera of Pipunculids and Platypezids there are present both claspers and what I became convinced are true gonopods. In a new search back through the lower Brachycera to families previously ignored I came upon interesting evidence in both the Cyrtidae and the Scenopinidae to support this. In these families are structures similar to those in the Muscoidea. Distinct claspers are not apparent on the ninth tergum, but the structure of the sternal elements are important.

In the Cyrtid *Eulonchus tristis* Lw. (Fig. 2) there is a sternal element fused completely with the lateral elements, which apically have a semiarticulated appendage. The aedeagus is fused into this structure. These lateral elements are almost certainly the gonopods, coxites and styli.

In the window fly, *Scenopinus fenestralis* L. (Fig. 3) there are structures which are closely reminiscent of the form of higher Muscoids. There is at most a weak sternal element,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1. VILLA
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4. CHALARUS

Figs. 1–4. Male hypopygia. 1. *Villa* sp., sternal complex, dorsal view. 2. *Eulonchus tristis*, sternal complex; a, dorsal view; b, lateral view. 3. *Scenopinus fenestralis*, sternal complex; a, anterior view; b, lateral view. 4. *Chalarus spurius*, a, dorsal view of sternal complex; b, lateral view of hypopygium.

Abbreviations: A, aedeagus; AA, aedeagal apodeme; C, cercus; GC, gonocoxite; GS, gonostylus; P, penis; PG, pregonite; PV, penis valve; S, sternum; SS, surstylus; T, tergum.

with a pair of large lobes ventrally which seem to be unusual extensions of the base of the gonocoxites. For the remainder, there is excellent correspondence. The gonocoxite has a strong lobe extending up close to the aedeagus, and the gonostylus is a distinct apical appendage. To those familiar with the terminalia of Calypterae, the projecting lobe of the gonocoxite is comparable to the pregonite, and the gonostylus with the postgonite. The tripartite penis despite the more elaborate aedeagal apodeme is similar to the structure of Pipunculids. The lateral elements are almost certainly true penis valves, which in higher forms become completely fused into the penis to form the lateral plates sheathing the aedeagus. This correspondence is rather amazing, and yet the Scenopinidae are an isolated family with no definite relatives, and of rather unspecialized form. They may well be one of the few surviving primitive relatives of the Muscoid line.

The other more primitive forms are found among the Aschiza, relatives of the Syrphids: they are almost invariably parasitic in habit, and are to a considerable extent specialized for this mode of life. The least specialized families are the Platypezidae, and Pipunculidae, and among the genera considered to be primitive by taxonomists are *Microsania* and *Platypezina* in the former family, and *Chalarus* in the latter.

In the Pipunculid, *Chalarus spurius* Fall. (Fig. 4) there is some reduction of parts. The surstyli are fused with the ninth tergum but are joined by an inner sternal plate identified as the tenth sternum by its position. The gonopods are completely separate and lack the gonostyli. There is a narrow sclerotized band to indicate the ninth sternum, while the penis is apically tripartite as in *Scenopinus*, indicating the partial fusion of the penis valves with the aedeagus. Higher pipunculids have an even more reduced form, the gonopods having been twisted and reduced to semi-membranous lobes around the base of the penis, so that I had failed to recognize them in my earlier studies.

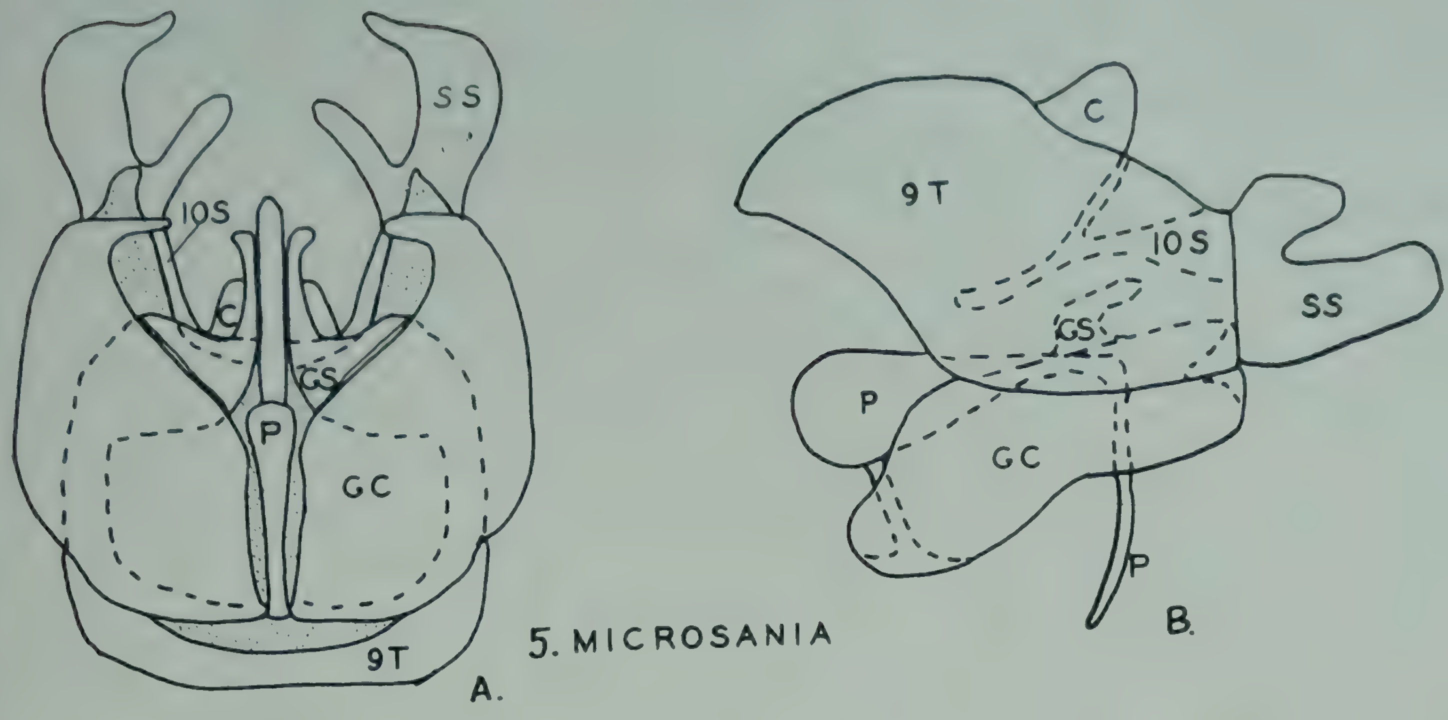
In *Microsania imperfecta* Lw. (Fig. 5) there is the typical ninth tergum. The lateral surstyli, somewhat bifurcate, are fused to the tenth sternum and articulate with the ninth tergum. The sternal complex is rather similar to that of the Cyrtid. Here however there is no distinct sternum. The two large lateral elements are the gonocoxites with an apical lobe, while the gonostyli are well set off as inner preapical articulated processes. Penis valves are not apparent.

In *Platypezina pacifica* Kess. (Fig. 6) the tenth sternum and surstyli are similarly connected. The sternal complex shows an anterior plate formed from the fused gonocoxites bearing on each side an anterior lobe, the pregonite, and a posterior process, the gonostylus or postgonite. At the base of the aedeagus are a pair of small processes, probably part of the penis valves. Here the gonocoxites have formed a smooth unbroken ring, having fused anteriorly with an unknown element of the ninth sternum and having been closed posteriorly by a sclerotization of the membrane enclosing the sternum dorsally.

To sum up the evidence to this point, these forms show recognizable gonocoxites and more rarely, gonostyli, in conjunction with the appearance of distinct and musculated surstyli. The ninth sternum is reduced or absent, and the gonocoxites tend to meet and fuse on the mid ventral line. Penis valves are present as processes partially fused with the aedeagus or, rarely, absent. The gonocoxites and gonostyli each form a pair of lobes around the base of the penis evident in most muscoids and homologous to the pre- and post-gonites of Crampton.

If these basic homologies are accepted, then the explanation of the structures of the muscoids is simplified greatly. The only reasonable alternative explanation of these structures that I can visualize is that the ninth sternum becomes completely divided in the midline and develops the various processes seen. Since the ninth sternum is almost always reduced and fused with the large coxites in the Lower Brachycera, it is unlikely that a reversal of proportions would occur in the muscoids. The musculature of the hypopygium is very complex, and I believe that no evidence for homologies on this basis is possible, lacking intermediate forms.

The basic plan as here presented makes it possible to identify the main elements in most higher forms. In the Syrphidae (Fig. 7) there is a retention of the long gonocoxites and small apical gonostyli, the gonocoxites having fused into a long tube around the penis, with the 9th sternum as an indefinite basal ventral element. There is no need of postulating, as Zumpt and Heinz did, a complete removal of the 9th segment ventrad to form this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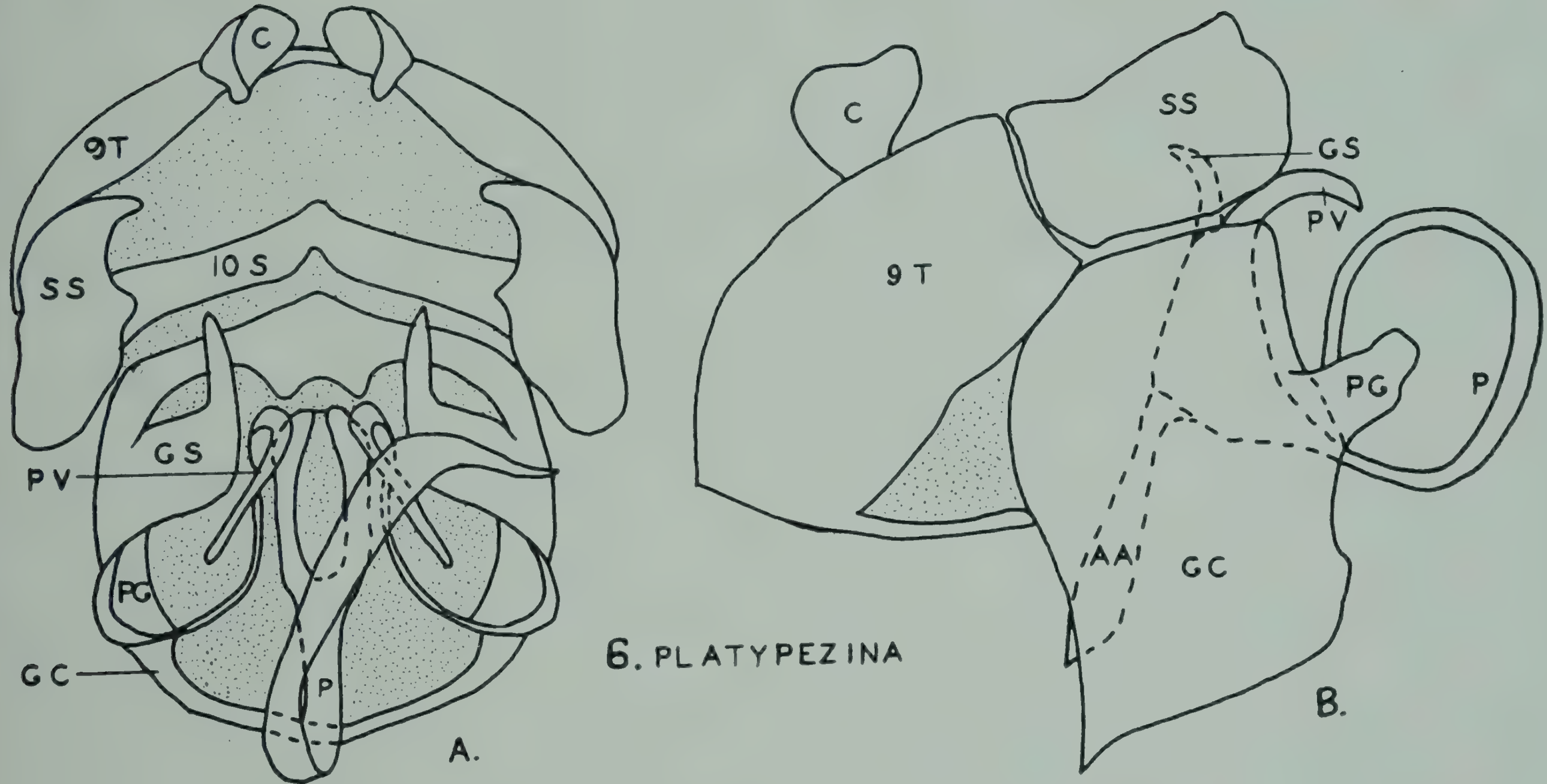
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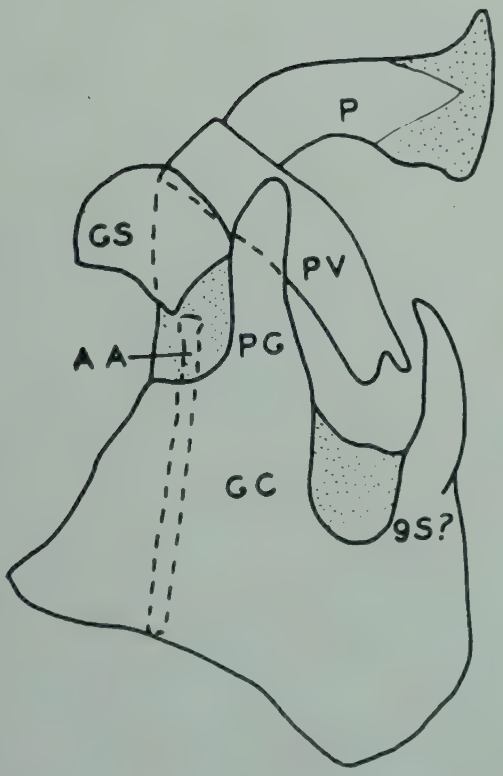
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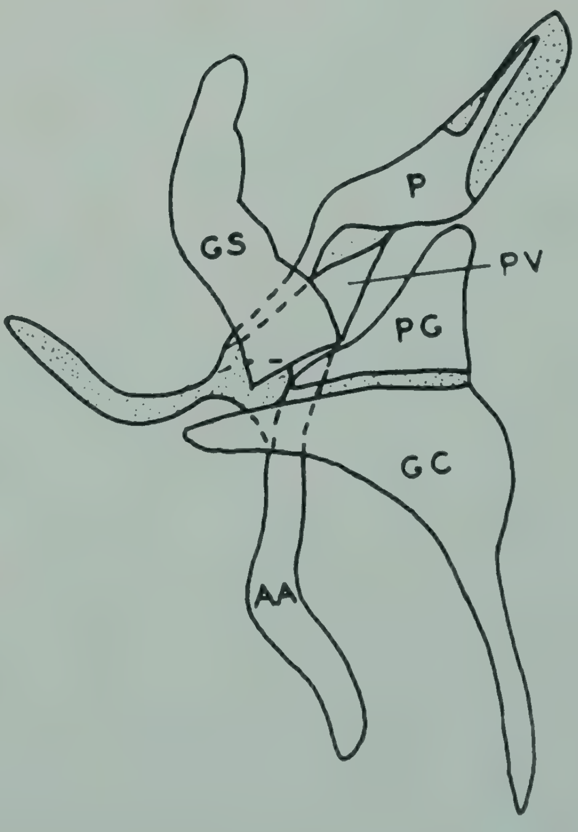
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8. MYDAEA

Figs. 5–8. Male hypopygia. 5. *Microsania imperfecta*, hypopygium; a, ventral view; b, lateral view. 6. *Platypezina pacifica*, hypopygium; a, posterior view; b, lateral view. 7. *Syrphus* sp., sternal complex, lateral view. 8. *Mydaea discimana*, sternal complex, lateral view. See Fig. 1 for abbreviations.

structure, with the 8th connecting directly to the 10th, which the dorsal part of the hypopygium was considered by them to be.

In the Acalypterae there is a great variety of structural modifications of the ventral elements, and it is not possible to discuss here even the main types. In the Calypterae this tenth sternum appears as slim rods (the bacilliform sclerites) or as small plates, or is completely absent due to a direct articulation of the sternal complex with the surstyli. There is usually a modification of the cerci to form well-sclerotized accessory claspers between the surstyli (the inner forceps of most workers), and in some of the higher muscoids, the surstyli and cerci are fused together.

The coxosternum is also further modified. As seen in *Mydaea discimana* Mall., (Fig. 8) a fairly typical form of the Muscidae, there is a strong sternal plate which is composed largely of the fused coxites, the pregonite lobe of the coxites appearing as a partially separated fragmentum. The gonostylus assumes a posterior position at the base of the penis, articulating with it at its posterior edge. The aedeagal apodeme is probably the fused apodemes of the penis valves, while the penis valves themselves form the sclerotized areas at the base of the penis.

REFERENCES

Crampton, G. C. 1923. The genitalia of male Diptera and Mecoptera compared with those of related insects from the standpoint of phylogeny. *Trans. Am. Ent. Soc.* 48: 207–25.

Crampton, G. C. 1938. The structure called parameres in male insects. *Bull. Brooklyn Ent. Soc.* 33: 16–23.

Crampton, G. C. 1942. The external morphology of the Diptera. Diptera of Connecticut, Fasc. 1: 10–165. Hartford, Conn.

Graham-Smith, G. S. 1938. The generative organs of the blow-fly *Calliphora erythrocephala* L., with special reference to their musculature and movements. *Parasit.* 30: 441–76.

Hennig, W. 1936. Beitrage zur Kenntnis des Kopulationsapparates der cyclorraphen Dipteren. Z. *Morph. Oekol. Tiere* 31: 328–70.

Zumpt, F., & H. Heinz. 1949. Studies on the sexual armature of Diptera. I. A contribution to the study of the morphology and homology of the male terminalia of *Eristalis tenax* L. (Syrphidae). *Ent. Mon. Mag.* 85: 299–306.

Zumpt, F., & H. Heinz. 1950. Studies in the sexual armature of Diptera. II. A contribution to the study of the morphology and homology of the male terminalia of *Calliphora* and *Sarcophaga* (Dipt., Calliphoridae). *Ent. Mon. Mag.* 86: 207–216.

DISCUSSION

C. W. SABROSKY. Is the bifurcate condition sometimes seen in the surstyli a possible indication that the tergum is derived from segments IX+X, rather than from IX alone?

J. G. T. CHILLCOTT. Yes, this is quite possible, but there is no further evidence, certainly not on the basis of musculature. In the meantime it seems easier to accept a simple structure.

GEO. STEYSKAL. In the more primitive Acalyptratae there is persistent evidence of anterior and posterior surstyli, which I interpret as evidence of two somites in the hypopygium (epandrium).

The Male Reproductive System of the Army Ant, *Eciton hamatum* Fabricius

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ABSTRACT

The two testes lie in the anterodorsal region of the gaster. Each testis is enclosed in a testicular capsule and consists of about 20 long follicles, which open into a reservoir at the anterior end of the vas deferens. Long, tightly coiled, tubular accessory glands lie one on either side of the gaster posterolaterad of the testes. The narrow, posterior ends of the vasa deferentia open into the beginnings of the ducts of these accessory glands. The ducts of the accessory glands meet on the dorsal, posterior region of the ventriculus. From this meeting point almost to the end of the system, they continue separate but are bound together by circular muscle. Anatomically, they appear as one tube, which is designated the bound accessory gland ducts. The bound accessory gland ducts encircle the ventriculus five or six times in an anterior direction and then turn posteriorly. They course along the lower part of the gastral cavity and pass through the dorsal, anterior opening in the lamina annularis of the genitalia. Toward the end of the bound accessory gland ducts, the lumina unite to form the ejaculatory duct. This duct opens into the dorsal, posterior side of the aedeagal bladder. There is a slender, chitinous wedge in its lumen. The aedeagal bladder opens posteriorly between the inner genitalic valves. Spermatozoa fill the lumina of the vasa deferentia except for the last portions, and sperm are found in the proximal ends of some testicular tubules.

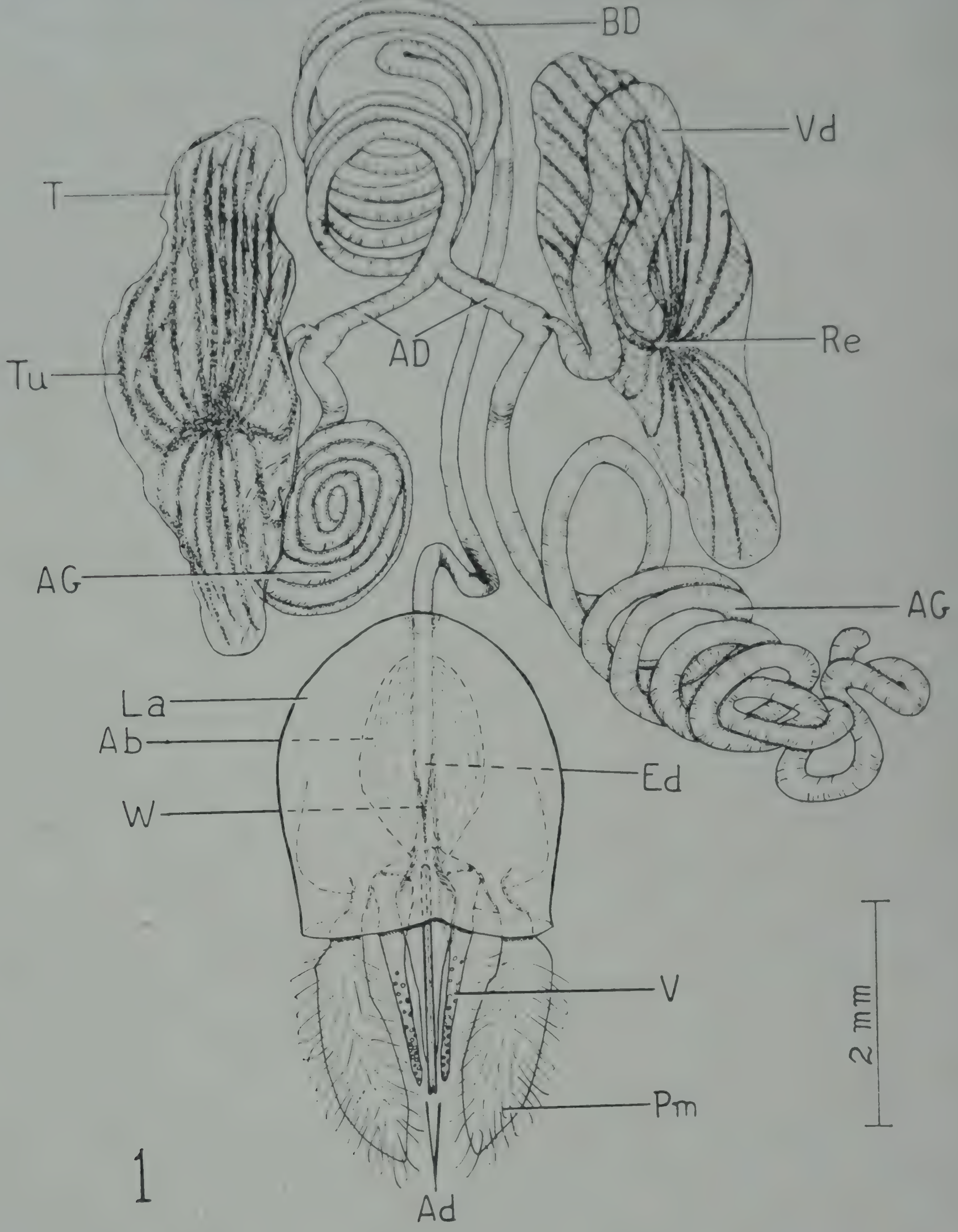
This description of the male reproductive system of *Eciton hamatum* Fabricius is the first description to be made for any species of this genus. It is the second report of a male system of a doryline ant; the male system of *Dorylus labiatus* Schuck has been previously described (Muckerjee, 1927).

The material for this study was collected by T. C. Schneirla on Barro Colorado Island in the Panama Canal Zone during 1948 (Schneirla and Brown, 1950). It was fixed in Bouin's fluid for 12 to 24 hours and then stored in 70 percent alcohol. Whole mounts of the system were stained with borax carmine. Sections of the gastral viscera were prepared by dehydrating with normal butyl alcohol (Lee, 1937, sect. 127) and embedding in 56–58 degree paraffin; they were then cut at 10 micra and stained with Harris' haematoxylin and triosin.

The system consists of the testes and vasa efferentia, the vasa deferentia, the accessory glands, the ducts of the accessory glands and the bound accessory gland ducts, the ejaculatory duct, the aedeagal bladder, and the external genitalia (Fig. 1). The external genitalia lie below the rectum and anus of the digestive system and in a large space within the last few gastral segments. Occasionally the posterior tips of the large, outer genitalic valves can be seen protruding from the hind end of the body. The external genitalia of this species has been reviewed recently (Borgmeier, 1955).

The testes are prominent organs, which lie in the anterodorsal region of the gaster, and they extend from the first into the third gastral segment. Each testis consists of approximately 20 long, slender, tapering tubules which converge toward the center or slightly posterior to the center of the testis. The free ends of the tubules are slightly narrower than the proximal ends. The proximal end of each tubule continues into a short, somewhat constricted portion, the vas efferens. The vasa efferentia in turn are collected into a common chamber, the reservoir, which is the first part of the vas deferens. A testicular capsule, richly supplied with tracheae, surrounds and covers the testicular tubules of each testis. The two capsules fit closely along their median surfaces, but they are not joined. In *D. labiatus*, each testis contains "a fair number" of small, tubular follicles, and no testicular capsule is present (Muckerjee, 1927).

The vas deferens of each side, located on the ventral side of the testis, is a wide, U-shaped tube. It extends anteriorly from the reservoir to the margin of the testicular capsule, loops backward for nearly an equal distance, and turns medially to join with the duct of the accessory gland. The last portion of the vas deferens is tapered and its diameter is sharply reduced. The testicular capsule covers all but the last portion of the vas deferens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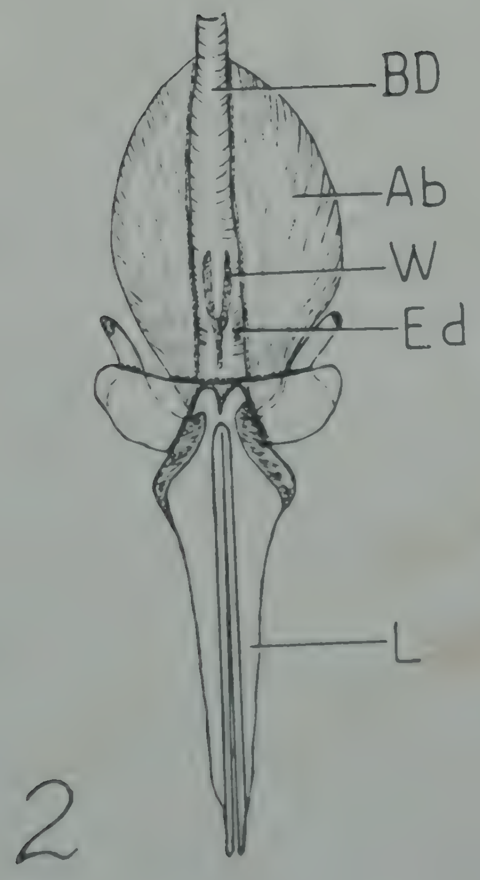

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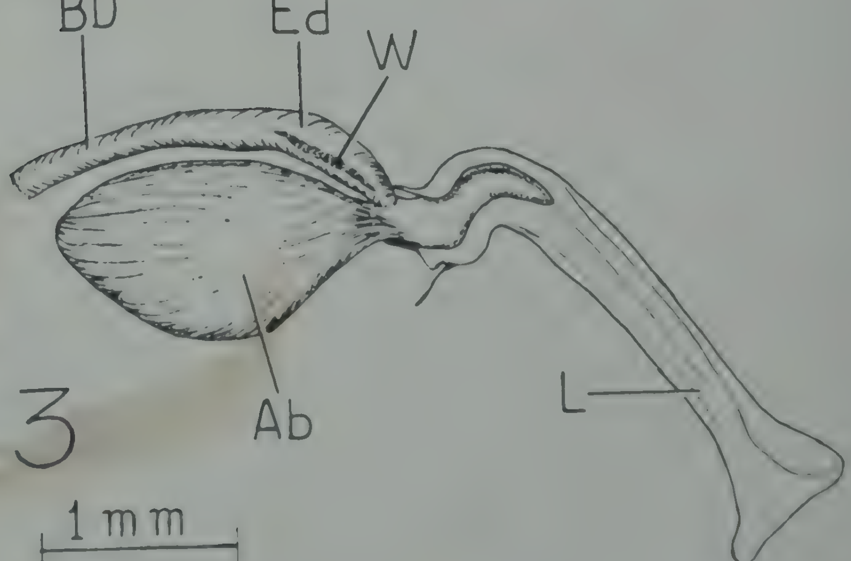
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(Figs. 1, 4). In *D. labiatus*, the corresponding structure is called a seminal duct. This duct extends from the testis into the base of the accessory gland. However, this seminal duct is divided into an anterior, narrow vas deferens portion and a much wider, posterior portion called the vesicula seminalis. There is a spherical dilation at the anterior end of the vas deferens portion, the collecting sac.

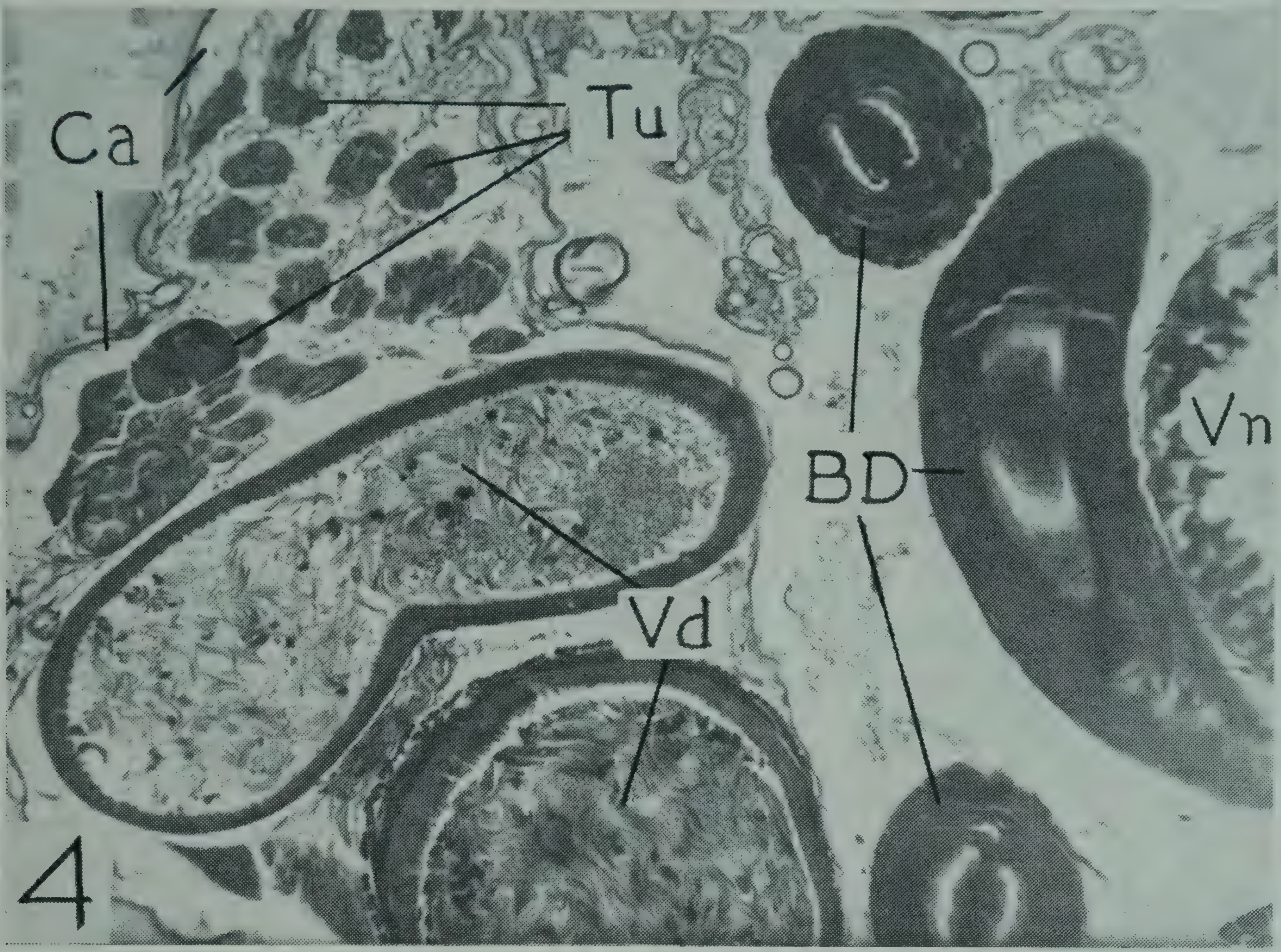

Fig. 4. Photomicrograph of a cross section of a portion of the gastral viscera. ×110. Abbreviations: BD, bound accessory gland ducts; Ca, testicular capsule; Tu, testicular tubules; Vd, vas deferens filled with spermatozoa; Vn, ventriculus.

The accessory glands are long, tightly coiled tubes situated one on either side of the gaster, posterolaterad of the testes and just in front of the large, cup-shaped lamina annularis or basal ring of the external genitalia. Uncoiled, these glands measure about 28 mm. in length. As the proximal loop of each gland proceeds in a dorsal direction and medially to form the duct portion, there is a slight swelling; it is here that the constricted end of the vas deferens enters the accessory gland duct (Fig. 1). The two ducts then continue medially and anteriorly to meet near the midline of the gaster in the dorsal, posterior region of the ventriculus and ventral to the testes. As the ducts meet, they are bound together by circular muscle. Anatomically, the bound accessory gland ducts appear to be one tube from this point to the end of the system, but, histologically, it is evident that the two

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Fig. 1. Dorsal view of the male reproductive system and genitalia of *Eciton hamatum* Fabricius. The testes are slightly more posterior than normal, the right testis is turned over to show the position of the vas deferens on the ventral side, and the right accessory gland is uncoiled.

Fig. 2. Dorsal view of the last portion of the reproductive system. Only the inner pair of genitalic valves, the laminae aedeagales or aedeagus, is included. The position of the wedge in the ejaculatory duct is indicated.

Fig. 3. Lateral dissection of the posterior end of the reproductive system. The right inner genitalic valve has been removed. The position of the wedge in the ejaculatory duct is indicated.

Figs. 2 and 3 are drawn to the same scale. Abbreviations: Ab, aedeagal bladder; AD, duct of accessory gland; Ad, aedeagus; AG, accessory gland; BD, bound accessory gland ducts; Ed, ejaculatory duct; L, lamina aedeagalis; La, lamina annularis; Pm, paramere of outer valve; Re, reservoir; T, testis; Tu, testicular tubules; V, volsella; Vd, vas deferens; W, wedge.

ducts continue separate while bound together with circular muscle (Figs. 1, 4). The bound accessory gland ducts continue in an anterior direction and encircle the ventriculus five or six times. In most cases, after circling the ventriculus a few times, the direction is reversed, e.g., from left to right, and the ventriculus is encircled a couple of times more in the opposite direction. Still bound together, the ducts bend ventrally and proceed posteriorly along the lower part of the gastral cavity. When they approach the lamina annularis of the external genitalia, they bend sharply dorsally, pass through the dorsal, anterior opening in the lamina annularis, and continue over the dorsal surface of the aedeagal bladder. The length of the bound accessory gland ducts measures about 28 to 31 mm. About half-way through the lamina annularis, the lumina of the ducts unite into a common lumen; this forms the ejaculatory duct. A slender, chitinous wedge is situated in the lumen of the ejaculatory duct (Figs. 1, 2). The ejaculatory duct opens on the dorsal, posterior end of the aedeagal bladder at the base of the laminae aedeagales, the inner pair of genitalic valves (Fig. 3). In *D. labiatus*, the accessory glands are large, slightly curved, thick-walled tubes situated on either side of the abdomen. They join medially to form a long, common duct, the ejaculatory duct. Muckerjee states, "a pair of chitinous penes is present on its ventral surface near the terminal opening of the duct". These he shows in his figure 2 as a slender, wedge-like structure at the posterior end of the ejaculatory duct. This chitinous wedge in the ejaculatory duct has been reported in other ants (Forbes, 1954).

The aedeagal bladder is an ellipsoidally-shaped, muscular sac located below the posterior end of the bound accessory gland ducts and the ejaculatory duct. It opens posteriorly between the inner genitalic valves. No mention is made of an aedeagal bladder in *D. labiatus*.

In *E. hamatum*, some spermatozoa are found in the proximal ends of some testicular tubules, and sperm fills the lumina of the vasa deferentia (Fig. 4). There is no sperm, however, in the constricted, proximal ends of the vasa deferentia or anywhere else in the system. Muckerjee found sperm in the vas deferens portion of the seminal ducts of *D. labiatus*. He states that the vesicula seminalis acts as a sperm reservoir.

REFERENCES

Borgmeier, T. 1955. Die Wanderameisen der Neotropischen Region (Hym. Formicidae). Studia Entomologica, Nr. 3. *Editora Vozes Limitada*, Petrópolis, R. J., Brasil.

Forbes, J. 1954. The anatomy and histology of the male reproductive system of *Camponotus pennsylvanicus* DeGeer (Formicidae, Hymenoptera). *J. Morph.* 95: 523–555.

Lee, A. Bolles. 1937. The microtomist's vade-mecum. 10th ed. *J. and A. Churchill Ltd.*, London.

Muckerjee, D. 1927. Digestive and reproductive systems of the male ant *Dorylus labiatus* Schuck. *Jour. Proc. Asiatic Soc. Bengal*, n.s., 22: 87–92.

Schneirla, T. C., and R. Z. Brown. 1950. Army-ant life and behavior under dry-season conditions. 4. Further investigation of cyclic processes in behavioral and reproductive functions. *Bull. Amer. Mus. Nat. Hist.* 95: 267–353.

DISCUSSION

P. J. HOLST CHRISTENSEN. 1. How big is the male army ant? 2. Have you a hypothesis regarding these peculiar accessory glands? Don't you think that the secretion of these glands is to be mixed with the testis products to make the sperm mobile?

JAMES FORBES. 1. The male of this species is about 2 cm. in length. 2. At the present I have no individual hypothesis concerning the accessory glands. It is assumed that the secretions of the glands of the reproductive system keep the sperm viable over long periods.

A Striking Peculiarity of the Male Reproductive Apparatus of *Spongiphora bormansi* Burr (Dermaptera)

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In dissecting some males of *Spongiphora bormansi* (Dermaptera-Labiidae) for cytological studies we found a particularly interesting reproductive apparatus, of which we give the following short report.

The testes, two cylindroid bodies, are circa 3mm long and 1.2mm in their major width. A rather thin deferent canal measuring about 9mm in length originates in the posterior extremity of each testes and finishes at the base of the seminal vesicle, where it opens with its congener. The seminal vesicle, a somewhat sinuous and relatively small organ, becomes a little thinner at the opposite extremity, there giving rise to a thick tube which, after making some irregular turns, opens into a strong ejaculatory pump. The latter is much larger than the testes, being circa 5mm long and 1.5mm wide in its median portion. The distal end of the ejaculatory pump becomes progressively thinner and is transformed into an enormously long ejaculatory cord, which alone justifies the present note. This cord, which measures about 150mm in length, makes some 23 lax turns around the digestive tract, going in loose spirals from the anterior to the posterior part of the

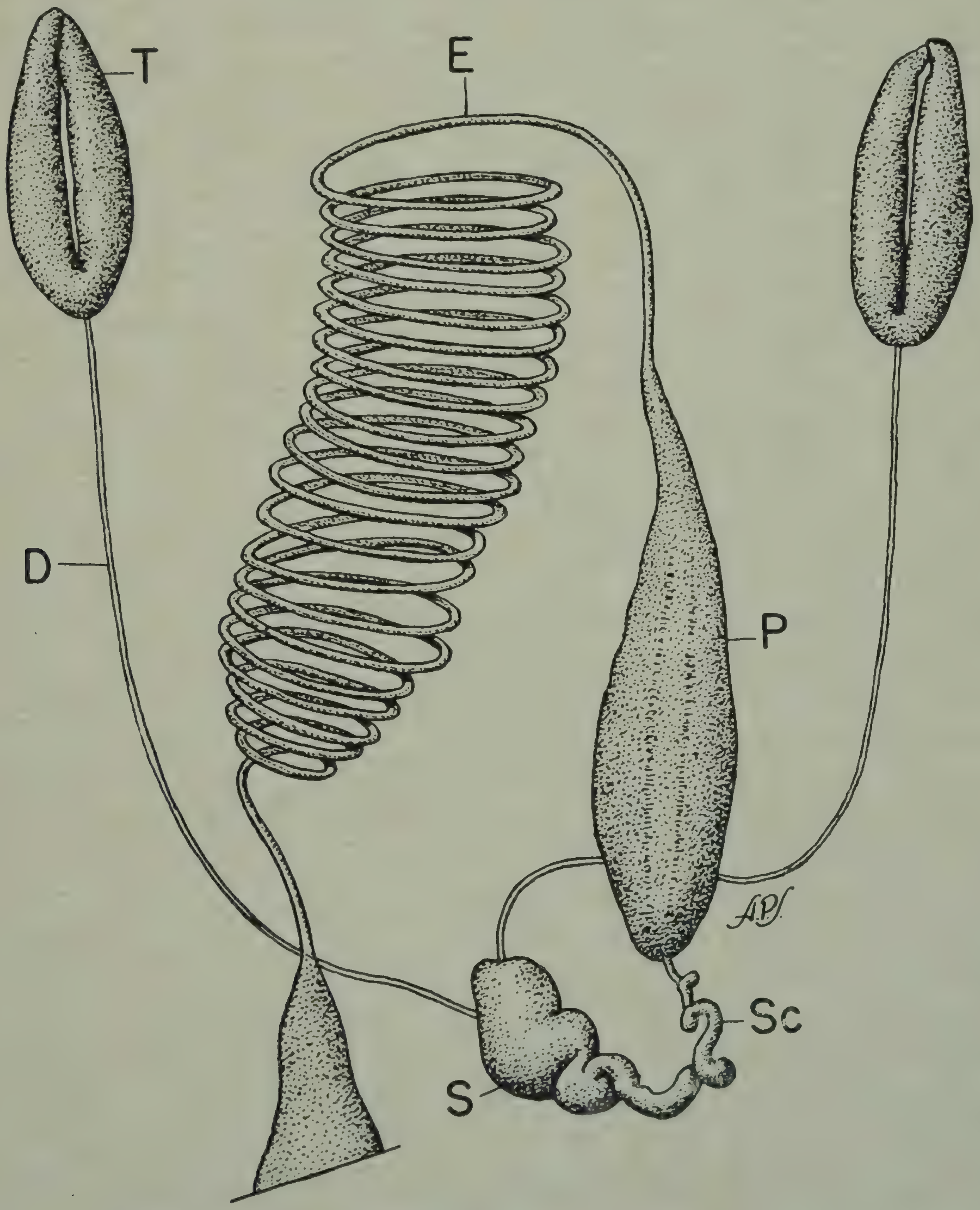

Fig. 1. Male reproductive apparatus of *Spongiphora bormansi*.

T, Testis; D, Deferent canal; S, Seminal vesicle; Sc, Seminal canal; P, Ejaculatory pump; E, Ejaculatory cord containing the ejaculatory duct.

abdominal cavity, where, becoming progressively thicker, it makes its way to the base of the aedaegus. These spirals have a considerable diameter and lie just beneath the walls of the abdomen, leaving the digestive tube entirely free in their middle.

The ejaculatory cord is formed by the ejaculatory duct, which, together with two tracheal tubules and two chitinous threads, runs along its whole length. The ejaculatory duct before entering the ejaculatory cord makes within the distal part of the ejaculatory pump a very convoluted ejaculatory glomerules.

Better than any description our figure shows the remarkable peculiarity of the reproductive apparatus of *Spongiphora bormansi*.

Histological and Histochemical Studies of Yolk Synthesis in Insects

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University of California
Berkeley, California

ABSTRACT[1]

The tremendous success of insects as competitors of man is due, in no small measure, to their tremendous reproductive capacity. Insect eggs are not only produced in large numbers but are also well endowed with yolk.

During the latter part of the 19th Century and during the first quarter of the present Century, many important contributions were made to our understanding of the histology of the insect ovary. However, little is known about insect yolk. Since 1930 the field of histochemistry has become systematized to the extent that it is now an important research tool. The purpose of this talk is to demonstrate the value of intergrating histochemical methods with the usual histological and morphological techniques in the investigation of yolk synthesis of insects. In undertaking a project on yolk synthesis, I had four main objectives in mind: (1) to characterize cytologically and chemically insect yolk; (2) to determine the origin of the nutritive substances in the egg and to trace the precursors of these substances back to the nurse tissues; (3) to uncover the extent of physiological specialization in the two types of nurse tissues found in the insect ovary; (4) to correlate the structural changes in ovarian cells with the physiological activities of these cells. The telotrophic ovarioles of Oncopeltus fasciatus *and* Tenebrio molitor *have been studied, as well as the polytrophic ovarioles of* Anisolabis maritima *and* Apis mellifera. *Most of this talk will be drawn from research on* Oncopeltus *and* Anisolabis.

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[1] Most of the material presented in this paper has been incorporated in an article in *Annual Review of Entomology*, vol. 3; 137–160. 1958.

Etude préliminaire des Glandes salivaires de *Macrosiphum solanifolii* Ashm. (Homoptera: Aphididae): Anatomie et Histologie

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RÉSUMÉ

Les glandes salivaires de Macrosiphum solanifolii *se présentent sous la forme de glandes en masse dont chacune des moitiés symétriques comprend une glande principale reliée à une glande accessoire antérieure.*

La glande accessoire comprend un seul type de cellules sécrétrices, tandis que la glande principale en comprend au moins cinq types différents. Ces types histologiques rappellent ceux décrits par Pesson (1944) chez les Coccides, mais chez ces derniers, ils sont anatomiquement distincts et forment des lobes séparés, tandis qu'ils sont concentrés en une glande massive et compacte chez les pucerons.

Les glandes salivaires des Aphididae ont été peu étudiées du point de vue physiologique et même histologique. Ces insectes étant considérés comme les vecteurs des maladies à virus des végétaux, l'étude de leurs glandes salivaires est cependant fondamentale pour aborder cet important problème de la transmission des viroses végétales.

Nous donnerons ici une étude préliminaire de l'anatomie microscopique et de l'histologie des glandes salivaires de *Macrosiphum solanifolii* Ashm., le puceron de la pomme de terre.

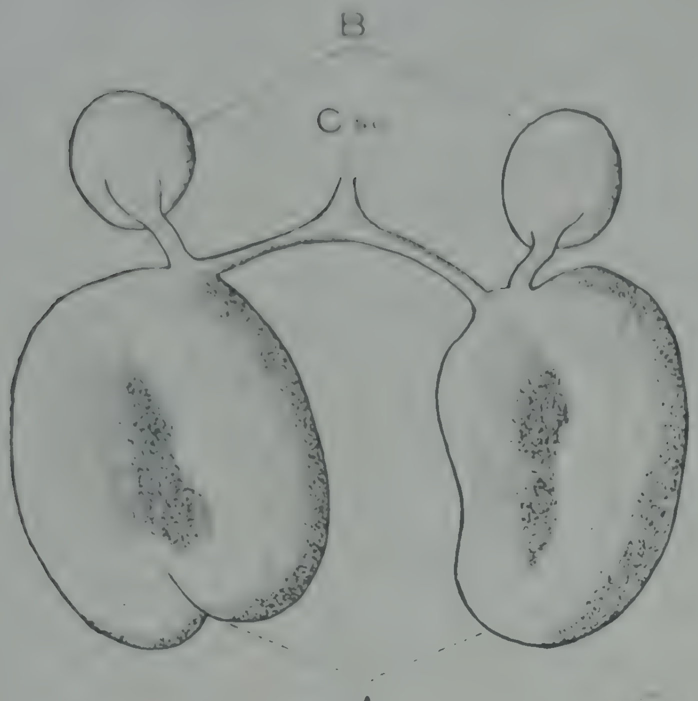
Ces glandes sont du type de glandes en masse (Fig. 1). Chacune des moitiés symétriques de la glande est composée d'un lobe principal légèrement ovoïde et réniforme (Fig. 1, A) et d'un lobe accessoire antérieur (Fig. 1, B) relié au précédent par un canal excréteur particulier. (L'aspect réniforme est difficilement observable sur pièces entières, car le lobe glandulaire est plus ou moins aplati et sur de telles préparations il se présente toujours selon sa plus grande surface). Les canaux excréteurs principaux convergent en un canal salivaire impair et médian, (Fig. 1, Csc) aboutissant à la pompe salivaire. Cet aspect anatomique est tout à fait comparable à celui que Weber (1928) a décrit pour un autre aphide, *Aphis fabae* Scop.

Par analogie avec ce qui a été décrit chez les femelles de Coccides (Pesson 1944), on peut penser que le petit lobe antérieur de chacunes des glandes paires pourrait représenter une partie maxillaire des glandes salivaires, le lobe principal étant une glande labiale. Mais, pour l'instant, chez l'espèce d'aphide étudié, nous n'avons pu préciser l'innervation de deux lobes glandulaires.

L'histologie révèle que chacune des glandes du lobe principal et du lobe accessoire est entourée d'une séreuse dépourvue de musculature. Elle se colore intensément par le vert lumière. (Coloration: hémalun, ponceau de xylidine, acide phosmolybdique, vert lumière, selon la technique de Patay, 1934).

GLANDES ACCESSOIRES ANTÉRIEURES

Les cellules de cette glande (Fig. 2) ont un cytoplasme granuleux et uniformément coloré par le rouge ponceau, les granulations cytoplasmiques étant cependant légèrement plus foncées que le fond même du cytoplasme. Celui-ci est creusé de nombreuses vacuoles, les plus grandes pouvant atteindre la taille même du noyau. Certaines vacuoles se forment étroitement en contact avec le noyau et apparemment même dans le noyau. On observe souvent que les plus grosses vacuoles sont entourées d'amas plus chromophiles et plusieurs images laissent l'impression que la destruction nucléaire en serait l'origine. Le noyau est volumineux, son contour est tantôt régulièrement ovoïde, tantôt fortement crénelé ou déformé. La chromatine se présente sous forme d'amas de dimensions assez uniformes régulièrement répartis. Chaque noyau héberge en outre, un ou plusieurs nucléoles qui peuvent atteindre une grande dimension. Il est possible que les noyaux participent directement par leur destruction à la sécrétion cellulaire. Toutefois des techniques histologiques



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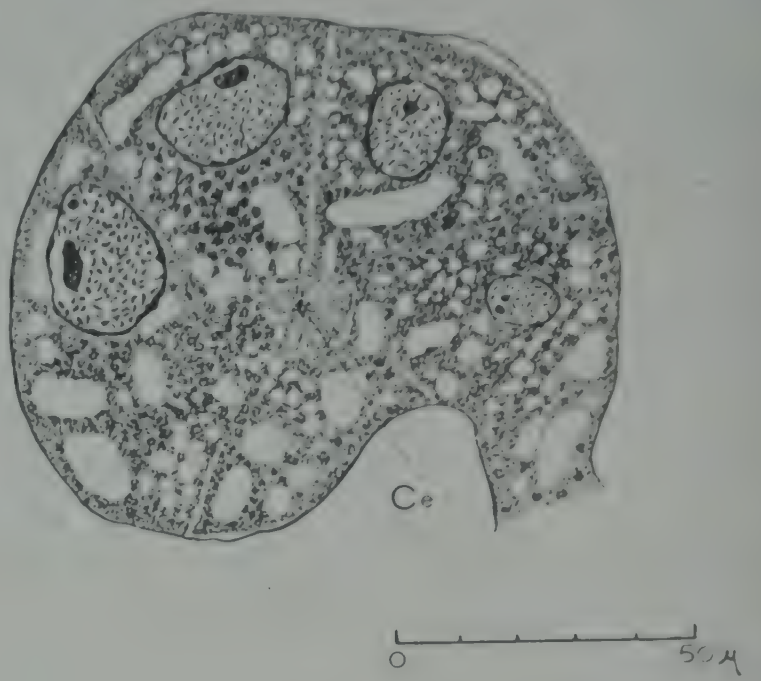

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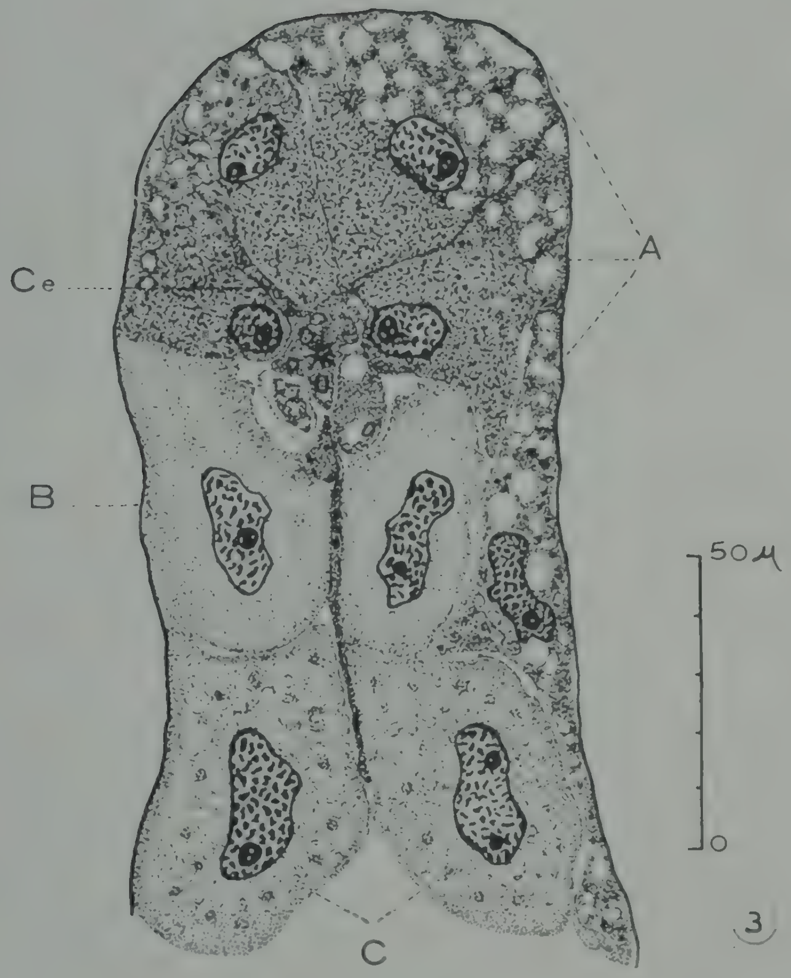

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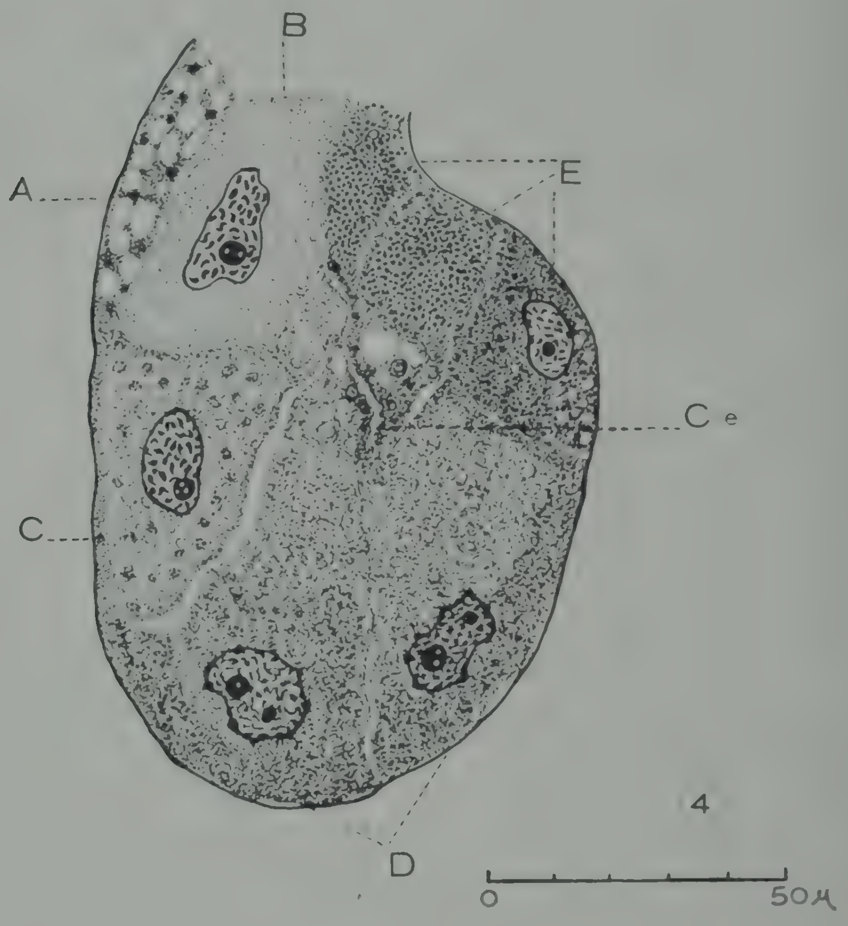

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particulières doivent être appliquées à l'étude de ces noyaux avant d'affirmer la réalité d'un tel processus.

GLANDES PRINCIPALES

La glande principale ou postérieure est formée par la coalescence d'au moins cinq types cellulaires différents, qui se distinguent nettement par leurs caractères histologiques.

Dans la partie antérieure de la glande, on trouve un premier groupe de cellules que nous décrivons ici comme type A (Fig. 3). Ces cellules comportent dans leur cytoplasme une partie corticale fortement vacuolisée, tandis que la partie apicale présente une structure granuleuse qui se colore uniformément et intensément au moyen du vert lumière. Les granulations elles-mêmes sont cependant ponceauphiles, la trame cytoplasmique seule étant colorée en vert. Le noyau qui renferme toujours un gros nucléole est fréquemment situé à la limite de ces deux parties cellulaires.

En arrière de ces cellules et plus spécialement localisé sur la face médiane des glandes, on observe un deuxième type glandulaire, type B (Fig. 3). Les cellules de ce type ont un cytoplasme très homogène, finement granuleux qui se colore uniformément par le ponceau en prenant une teinte brun-rouge. L'aspect général du cytoplasme est comparable à celui des cellules de la glande accessoire antérieure mais ne présente pas de vacuoles. Le noyau de forme très irrégulière offre des grains de chromatine généralement plus gros que ceux des cellules du type A. Il héberge normalement un nucléole. Dans certaines coupes, on observe des images laissant supposer un stade de dégénérescence des noyaux. Mais ce phénomène doit, avant d'être interprété, faire l'objet d'une étude particulière plus poussée.

Le troisième type cellulaire est anatomiquement placé en arrière des cellules précédentes, type C (Figs. 3 et 4). Le cytoplasme, d'aspect spongieux, est creusé de petites vacuoles assez régulières et très rapprochées, laissant entre elles une trame cytoplasmique qui se colore en brun rougeâtre. Dans la région basale des cellules, ces vacuoles paraissent remplies d'une substance rougeâtre, tandis que dans la région apicale, elles deviennent plus claires et prennent une teinte verdâtre.

Le quatrième type cellulaire, type D (Fig. 4), forme la partie postérieure de la glande principale. Ce sont de grandes cellules à cytoplasme homogène finement granuleux, se colorant uniformément en brun-rouge par le ponceau. A la partie basale des cellules, les granulations cytoplasmiques paraissent beaucoup plus denses. Le noyau est fortement crénelé, il héberge un ou deux gros nucléoles. La chromatine en est finement dispersée et réunie par des fibrilles en réseaux.

Enfin dans la région du hile de la glande principale, on observe quatre petites cellules très particulières, fortement chromatiques, type E (Fig. 4). Ces cellules ont un cytoplasme à grosses granulations très denses, se colorant en rouge jaunâtre. Cependant la partie basale de ces cellules paraît légèrement vacuolaire et a tendance à se colorer au moyen du vert lumière. Sur des coupes de glandes salivaires d'embryon d'aphide, ces cellules très spéciales se retouvent aisément.

Le canal excréteur (Figs. 2, 3 et 4, Ce) est un fin canal dont la lumière cylindrique est bordée d'une intima chitineuse qui est coloré en vert-jaune par le vert lumière. Le cytoplasme des cellules épithéliales qui entoutent le canal présente une structure fibrillaire disposée radialement autour du canal excréteur.

CONCLUSION

La multiplicité des types histologiques que nous venons de décrire chez les aphides rappelle de très près ce qui a été décrit par Pesson (1944) chez les Coccides. Mais, alors que chez ces derniers les divers types cellulaires sont anatomiquement distincts, formant huit lobes séparés, ici on assiste à une concentration très poussée aboutissant à une glande massive et compacte.

Cette étude n'est qu'une première approximation de la structure des glandes salivaires des aphides. Nous envisageons de la compléter par des études cytologiques beaucoup plus précises où nous ferons intervenir des techniques permettant d'analyser la physiologie de ces glandes salivaires.

BIBLIOGRAPHIE

Patay, R. 1934. Une nouvelle technique de coloration histologique. *Bull. d'hist. appl.* 10, Paris.

Pesson, P. 1944. Contribution à l'étude morphologique et fonctionnelle de la tête, de l'appareil buccal et du tube digestif des femelles de Coccides. *Monographies, Centr. Nat. Rech. Agr. Paris*, 266 p., 152 fig., 1 pl.

Weber, H. 1928. Skelett, Muskulatur und Darm der schwarzen Blattlaus *Aphis fabae* Scop. mit besondere Berücksichtigung der Funktion der Mundverkzeuge und des Darmes. *Zoologica* 28: 5–118.

Alary Musculature as a Basis of the System of Pterygote Insects

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ABSTRACT

In 1923 Martynov proposed his well known system of Insecta Pterygota based on the resting position of wings and presence or absence of jugum. The system expounded in the present paper represents a further development of Martynov's ideas, though deviating rather considerably from his viewpoint.

Panorpoid and Hemipteroid complexes of orders may be united on account of their tendencies toward proboscis formation and forewing preponderance, though the former group is holo- and the latter hemimetabolous. Hymenoptera are to be included in the Panorpoids because of the erucoid larvae of their primitive forms, i.e. sawflies. By adding the Ephemeroids to the above two complexes the three would be united into the Anteromotoria subdivision.

On the contrary in the Orthopteroid and Coleopteroid complexes there is almost no proboscis formation tendency while, contrary to the Anteromotoria, the hindwing is preponderant in them. Accordingly they may be merged into the Posteromotoria subdivision.

Owing to the presence of dorsoventral and longitudinal dorsal muscles in both Antero- and Postermotoria the two subdivisions are united into Chiastomyaria division.

On the contrary in the Odonata the longitudinal muscles degenerate, their function being performed by the increased pleural ones. Accordingly the dragonflies should be regarded as Orthomyaria division.

It should be emphasized that the antero- and posteromotorism represent but tendencies as recorded in the respective subdivisions, since in the generalized members of the same groups a primitive bimotorism, i.e. equal development of both pairs of wings, may be retained.

The described data are shown in the vertical columns of the tabular system. The horizontal lines divide all the orders as follows. As Inferiores the orders are regarded which are morphologically generalized, often bimotoric and show no great numbers of species. On the contrary all the Superiores are either antero- or posteromotoric, their morphological specialisation reaches the highest level known and the number of species and biological types is the greatest in the animal world. Finally the Dealata show strongest tendency to the loss of wings and some narrow specialisations; the numbers of species and especially of the biological types are very small in them.

INTRODUCTION

The number of Pterygote Insect orders in most of the modern systems fluctuates about 30 and more, and the necessity to unite them into some larger units is naturally felt. The Panorpoid (Neuropteroid) complex is generally recognized. But, e.g. in the system accepted by Weber (1933, 1938), there are no large units besides the above complex, while some six of the suborders accepted by him consist of a single order each and thus cannot be regarded as unifying. Martynov proposed in 1923 a system in which all the orders were united into larger groups. His system is largely accepted in the Soviet literature and has penetrated into the foreign one as well (Grassé, 1949). It was remodelled several times by its author and is reproduced in Table I.

A similar system was proposed by Crampton (1929).

It is known that Martynov's division of Pterygota into Palaeoptera and Neoptera is based on the manner of the wing folding and the resulting structure of the wing. Both Martynov and Snodgrass suppose that the flight of insects originated from gliding movement in the air and accordingly the spread out position of wings at rest as in the Anisoptera is considered as primitive, the dorsal closing of wings in the Zygoptera and mayflies being regarded as an unimportant modification. The absence of jugum in the indicated forms is a sequel of their position of rest and they constitute accordingly the division Palaeoptera. Meanwhile the remaining Pterygota that constitute the division Neoptera do fold their

TABLE I. System of Pterygota by Martynov 1923–1938 (with some abbreviations from 1938 version).

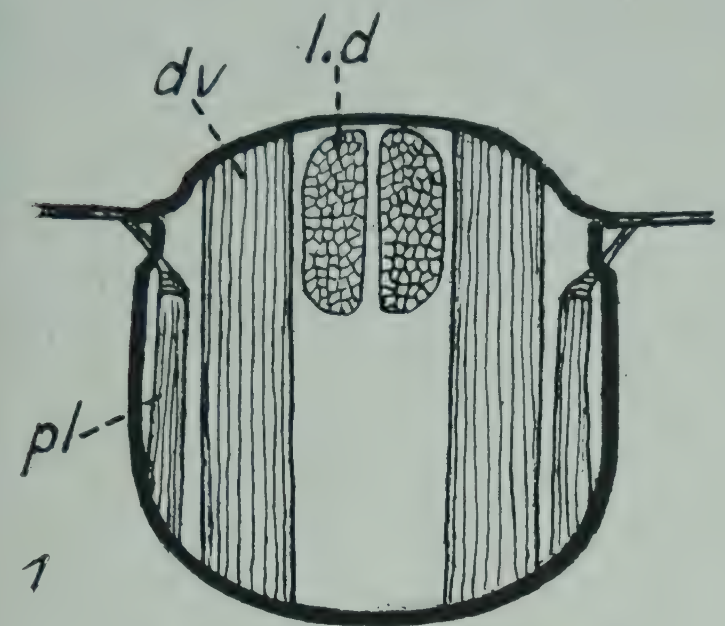
Divisio Palaeoptera			
		Ephemeroptera	
		Odonata	
Divisio Neoptera			
	Subdivisio Polyneoptera		
		Orthoptera saltatoria	
		Phasmatodea	
		Plecoptera	
		Embiodea	
		Dermaptera	
		Blattodea	
		Mantodea	
		Isoptera	
	Subdivisio Oligoneoptera		
		Coleoptera	
		Strepsiptera	
		Siphonaptera	
		Megaloptera	Coleoptera-Neuroptera
		Neuroptera	Hymenoptera
		Rhaphidioptera	
		Hymenoptera	
		Mecoptera	
		Diptera	Mecoptera-Diptera
		Trichoptera	
		Lepidoptera	Trichoptera-Lepidoptera
	Subdivisio Paraneoptera		
		Thysanoptera	
		Psocoptera	
		Mallophaga	Corrodentia
		Anoplura	
		Rhynchota	

wings along the body and show a more or less developed jugum, the latter representing a sort of adaptation to the indicated manner of wing folding. The Neoptera consist of three subdivisions: 1) Polyneoptera, comprising mainly orthoperoid groups and also termites, stoneflies and embiids, 2) Paraneoptera, the orders related to Hemiptera and Psocoptera and 3) Oligoneoptera, all the holometabolous groups.

The system to be dealt with in the present paper should be regarded as a further development of Martynov's ideas. In spite of the fact that his and the present author's views are somewhat at variance, the great value of three main results of Martynov's work should be especially emphasized. First, his system intentionally covers all the Pterygota on the basis of some general idea. Second, his juxtaposition of dragonflies to almost all other Pterygota reveals his very great insight. Third, his three subdivisions enumerated already are almost totally natural and their unity is high.

The modern theory of the origin of flight from gliding meets with some difficulties. First of all the long lateral paranota should encumber crawling. Martynov himself supposed that just this circumstance caused the extinction of many Palaeoptera groups. On the other hand, gliding in the recent insects serves as an auxiliary to flapping type of flight being observed only in strong flyers with wide wing surfaces like large dragonflies and large butterflies. Neither insects nor birds show gliding flight without flapping flight. No flight has developed from gliding as observed in a few mammals, lizards and frogs. But the origin of flight may be imagined otherwise. Suppose the paranota acquired the articulations and mobility first and then became elongate afterwards. If so, the running and crawling could be accelerated by the strokes of short movable paranota while the elongation of the latter would lead to a development of normal flapping flight. Such an auxiliary function of wings is observed, e.g. in *Bombyx mori* that has lost its flight. This viewpoint, although of course purely hypothetical, removes the difficulties of the gliding theory.

The manner of wing folding, so much stressed by the theory, represents, as a matter of fact, a very unstable character even in closely allied forms. A *Psychoda* holds the costae downwards, a *Phlebotomus* does so upwards, in a *Culex* the wings are held flat over the abdomen, in a *Tipula* they are spread out. The Geometridae are no less variable with re-



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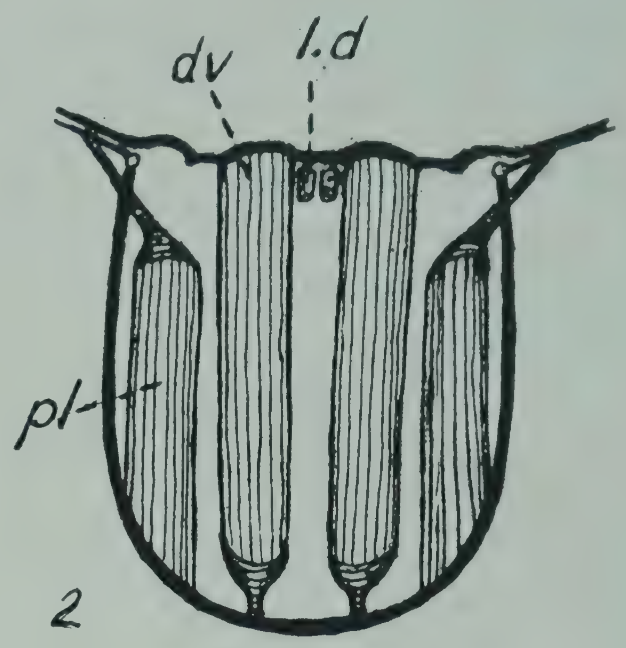

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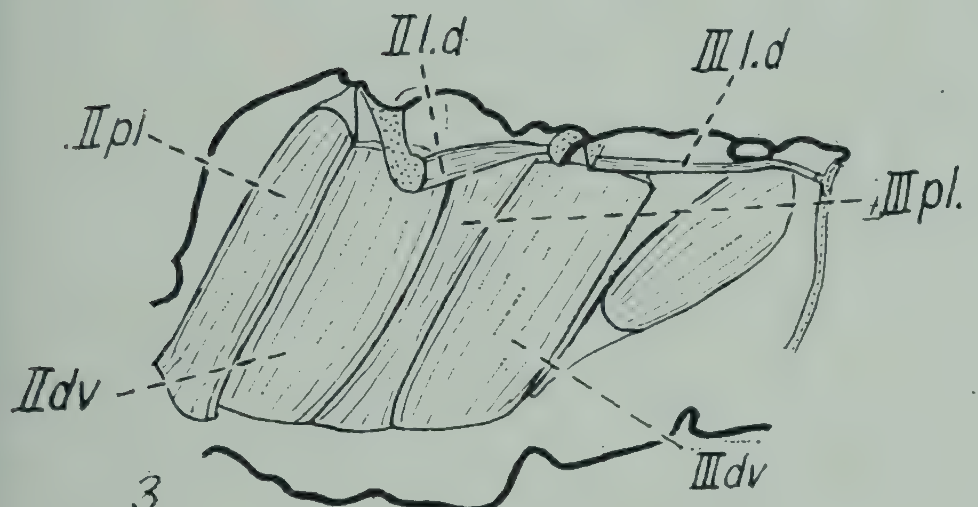
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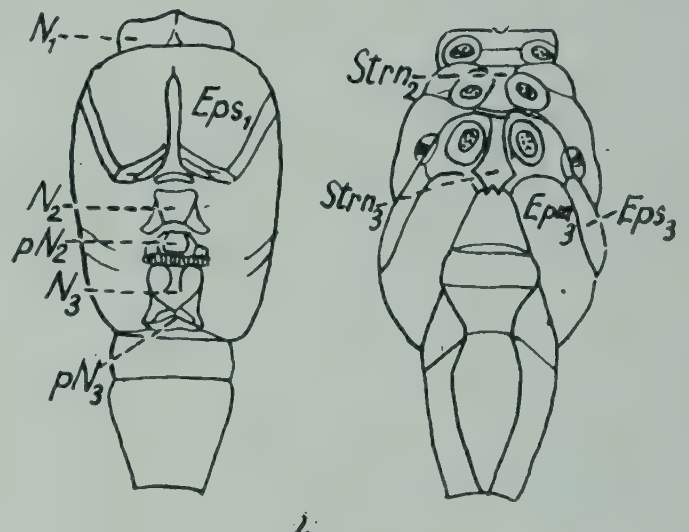
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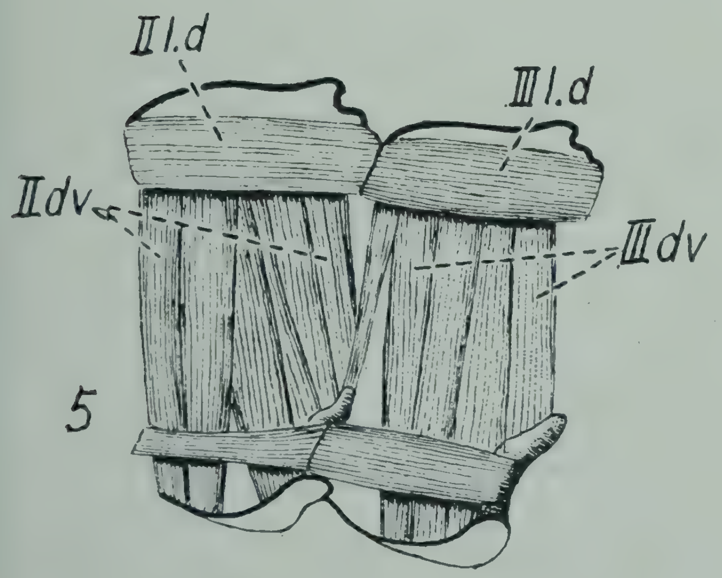
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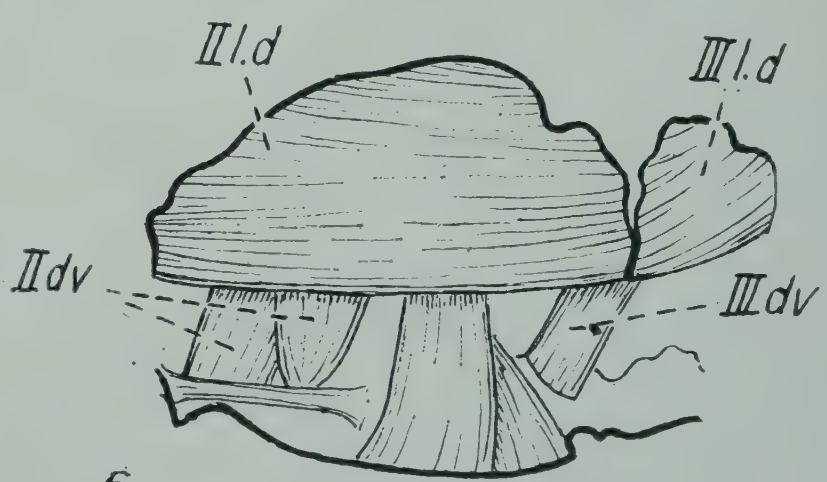
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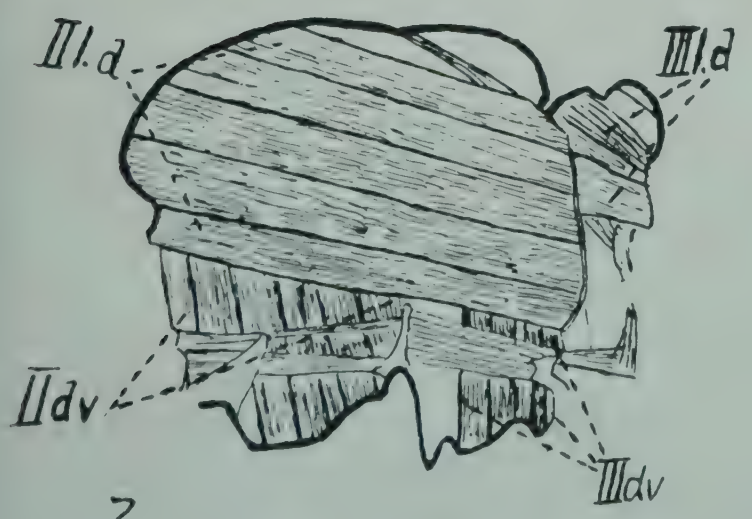
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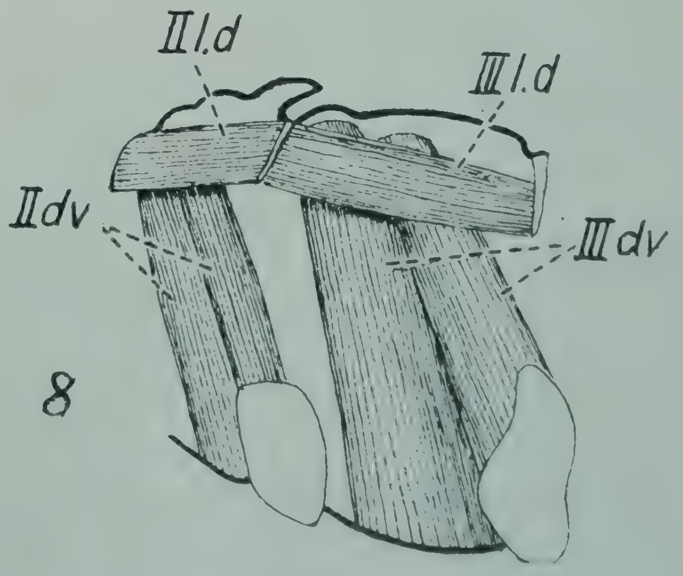
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II dv
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8

(See page 608 for captions).

gard to this. Thus evidently neither the character under consideration nor the venation supposedly dependent upon it can serve as a criterion to oppose dragonflies and mayflies to the rest of the Pterygota.

But the Odonata show another character that really leads to the juxtaposition in question. In the great majority of insects the alary musculature consists of powerful indirect dorsoventral and longitudinal dorsal muscles affording the main force to the stroke (Fig. 1, dv, l.d) and direct pleural musculature (pl) upon which the inclinations of wings during the stroke and the folding and spreading are dependent. Since the directions of the main muscles cross over each other, the muscular motor of this type suggests the name Chiastomyaria for the corresponding insects. But still Poletaiew (1881) has shown that the longitudinal dorsals are degenerate in the Odonata (Fig. 3, II l.d, III l.d) and have totally disappeared from the metathorax of the Libellulidae. His data are corroborated by Clark (1940). The function of the downstroke has passed from the longitudinals to the pleurals, the latter having developed greatly. The increase of pleural muscles is followed by the corresponding expansion of the pleural sclerites that cover them (Fig. 4, Emp_3, Eps_3) while the medial sclerites of the thorax, viz. sterna and terga, decrease strongly (N_2, Ni_3) so that the Odonata may be described as microtergal, microsternal and megapleural insects. Thus the direction of all the functionally important alary muscles of dragonflies is dorsoventral, the element of crossing over being minimized. Therefore the Odonata may be named Orthomyaria. Thus they really differ from the remaining insects.

The primitive Chiastomyaric forms, e.g., most of the Neuroptera, may be called bimotoric because their wings and alary muscles are more or less similar in both meso- and metathorax. There are two directions of specialisation starting from this status. In one of them the forewings become preponderant (Voss's Hymenoptera type, 1913), in another (as in the Coleoptera) just the opposite is the case. Accordingly the former forms are to be termed Anteromotoria, the latter Posteromotoria. Let us now see if the above consideration may be coupled with some other data to classify the orders of the Pterygota in a natural way.

Holometabolism and strong tendency toward proboscis formation are typical of the Panorpoid complex. As to the alary mechanism the Mecoptera and other primitive Panorpoids show a bimotoric condition, (Fig. 5), but in the higher orders anteromotorism becomes preponderant and reaches its peak in the Diptera. To the generally accepted array of Panorpoid orders that of the Hymenoptera should be added. The free living larvae of sawflies are undoubtedly eruciform since they are provided with labio-maxillar complex, labial silk glands and abdominal legs. Prominent development of the ovipositor in the imago and a general absence of the organ in Panorpoids do not interfere with the above idea since a rudiment of the orthopteroid ovipositor has been discovered in *Panorpa*

Fig. 1. Diagrammatic transverse section through Chiastomyaric thorax. dv—dorsoventral levator, l.d.—longitudinal dorsal depressor, pl—pleural muscle.

Fig. 2. Diagrammatic transverse section through Orthomyaric thorax. Combined after Weber and Clark. Letters as in Fig. 1.

Fig. 3. Longitudinal section through Orthomyaric bimotoric pterothorax of *Anax junius* (Odonata Anisoptera). After Clark, simplified. IIdv. IIIdv—meso- and metathoracal dorsoventral levators resp., II l.d. III l.d.—meso- and metathoracal longitudinal dorsal depressors resp., II pl, III pl—meso- and metathoracal pleural depressors resp.

Fig. 4. Thorax of *Austrophlebia*, left—dorsal view, right—ventral view. From Tillyard. Epm_3, Eps_3—epimeron and episternum of the metathorax. N_1, N_2, N_3—pro-, meso- and metanotum resp., pN_2, pN_3—meso- and metapostnotum resp., $Strn_2$, $Strn_3$—meso- and metasternum resp.

Fig. 5. Longitudinal section through Chiastomyaric bimotoric pterothorax of *Sialis* (Neuroptera). From We simplified. Letters as before.

Fig. 6. Longitudinal section through Chiastomyaric anteromotoric thorax of Mayfly. From Needham, Traver and Hsu, simplified. Letters as before.

Fig. 7. Longitudinal section through Chiastomyaric posteromotoric pterothorax of *Telea polyphemus* Cr. From Nüesch, simplified. Letters as before.

Fig. 8. Longitudinal section through Chiastomyaric posteromotoric pterothorax of adephagous beetle. From Weber, simplified. Letters as before.

(Grell 1942), while a typical ovipositor has long been known in *Rhaphidia*, a group considered by Martynov as related to the Hymenoptera.

Another anteromotoric complex is that of Hemipteroidea corresponding to Martynov's Paraneoptera. Around the primitive order Psocoptera the orders Hemiptera, Thysanoptera and Anoplura are concentrated. Like the preceeding group the tendency to sucking mouth parts is strong in the Hemipteroidea, but their proboscis is always piercing; this is usually not the case in the Panorpoids. Another distinction from the latter is the hemimetabolism of hemipteroids.

It is evident that on the basis of the tendencies to anteromotorism and proboscis formation the two enormous complexes may be put together. The mayflies are also to be added to them because of their wing mechanism being typically chiastomyaric and anteromotoric (Fig. 6). But owing to the tendency toward proboscis formation being totally lacking in the Ephemeroptera they should be considered as a third complex of the Anteromotoria. They are thus totally broken off from the orthomyaric Odonata.

One more natural complex is the Orthopteroid one. It consists of the orders considered as Orthoptera in the old systematics. At the present time the termites, stoneflies and Embioptera are attached to the group, which thus corresponds exactly to Martynov's Polyneoptera. Hemimetabolism and a total absence of the proboscis formation tendency are typical of the complex. Some of its orders, e.g. stoneflies, are bimotoric. But if a specialisation of the alary motor begins it is in a direction opposite to that observed in the Anteromotoria, that is, the hindwing becomes preponderant and, e.g. in some Phasmoptera, it is the only working one while the forewing undergoes a strong degeneration. Thus the posteromotoric tendency is evident in the Orthopteroidea. It is still more pronounced in the Coleoptera (Fig. 8) and reaches its climax in the Strepsiptera, the latter order in accordance with Ulrich (1944) being considered a branch of beetles (against Jeannel, 1945). The proboscis formation tendency, though present, is however very slight. A proboscis occurs in a few forms of the Meloidae. But owing to their holometabolism Coleoptera and Strepsiptera should be separated from the Orthopteroidea as a complex of Coleopteroidea. Both of them are combined into the Posteromotoria subdivision.

To sum up (Table II) all the Pterygota are divided into two divisions, viz. Orthomyaria and Chiastomyaria. The first of them consists of a single bimotoric subdivision with a single libelluloid complex and single order of the Odonata. The Chiastomyaria division includes anteromotoric and posteromotoric subdivisions, the former consisting of three, the latter of two, complexes. It should be emphasized first that the distribution of orders among the higher systematic units differs but little from that given by Martynov. Secondly, the differences in the alary motor, mouth parts and metamorphosis are largely concomitant. Thirdly, the terms of antero- and posteromotorism do not mean that all the members of a group exhibit the same type of alary musculature. The only meaning of the above terms is that a tendency to a definite direction of specialisation is typical of a given group.

TABLE II.

	ORTHOMYARIA	CHIASTOMYARIA				
	Bimotoria	Anteromotoria			Posteromotoria	
	LIBELLULOIDEA	EPHEMEROIDEA	HEMIPTEROIDEA	PANORPOIDEA	COLEOPTEROIDEA	ORTHOPTEROIDEA
Superiores 605.0			Hem 40.0	Dipt 85.0 Lep 140.0 Hym 90.0	Col 250.0	
28.9	Odon 3.5	Eph 1.0	Psoc 0.8	Mec 0.5 Tri 3.0 Neu 4.0		Blatt 3.7 Pha 0.7 Orth 10.0 Derm 1.0 Plec 0.7
			Ano 2.2 Thys 1.5	Aph 1.0	Str 0.17	Iso 2.6 Emb 0.6

Ano - Anoplura
Aph - Aphaniptera
Blatt - Blattoptera
Col - Coleoptera
Derm - Dermaptera
Dipt - Diptera
Emb - Embioptera
Eph - Ephemeroptera
Hem - Hemiptera
Hym - Hymenoptera
Iso — Isoptera
Lep — Lepidoptera
Mec — Mecoptera
Neur - Neuroptera
Odon - Odonata
Pha — Phasmoptera
Plec — Plecoptera
Psoc — Psocoptera
Orth — Orthoptera
Str — Strepsiptera
Thys - Thysanoptera
Tri - Trichoptera

Ciphers show number of species in thousands

The described classification of orders is shown in the proposed system by vertical columns. There are, however, horizontal dividing lines too. It is generally assumed that among the insects there are primitive, highly specialized and degenerate orders. This first is shown graphically by the horizontal partitions. For the orders of the Inferiores series a general primitivism which is not influenced by a few specialisations, if present, is typical. The number of species (indicated in thousands in Table II) and biological types is mostly not great, the body size varies from small and medium to very large. The five orders of the series of Superiores exhibit the maximum degree of morphological specialisation, the numbers of species and biological types are enormous, the body size fluctuates from minute to large and even gigantic. These five orders are undoubtedly the most highly specialized and most flourishing in the class of Insecta. In the series of Dealata general primitiveness is observed, coupled, however, with some high specialisations. There is a strong tendency to the loss of wings, the numbers of species are small, the number of biological types is very low and the body size may be considered as diminished except perhaps that of termites.

In the Panorpoid complex it is especially clear that the primitive orders of Mecoptera and Neuroptera represent a sort of centre which the highest orders of Diptera, Lepidoptera and Hymenoptera arise from on the one hand and the parasitic Aphaniptera on the other. Similar interrelations are observed in the Hemipteroid complex and Posteromotoric subdivision.

The whole of the table may be considered as a transverse section across the modern level of the phylogenetic phyla. Accordingly no extinct groups are included.

REFERENCES

Clark, H. W. 1940. The adult musculature of the anisopterous dragonfly thorax (Odonata Anisoptera). *Journ. Morph.* 67.

Crampton, G. C. 1929. The terminal abdominal structures of female insects compared throughout the order from the standpoint of phylogeny. *Journ. N.Y. Ent. Soc.* 37.

Grassé, P. P. 1949. Traité de zoologie. Paris, 9.

Grell, K. G. 1942. Der Genitalapparat von *Panorpa communis* L. *Zool. Jahrb. Anat.* 67.

Jeannel, R. 1945. Sur la position systématique des Strepsipteres. *Rev. Fr. Entom.* II.

Martynoff, A. 1924. L'évolution de deux formes d'ailes chez les insectes. *Rev. Zool. Russe* 4. (In Russian with French résumé).

Martynoff, A. 1925. Ueber zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. *Zeit. Morph. Oekol.* 4.

Martynoff, A. 1938. Études sur l'Histoire Géologique et la Phylogénie des Ordres des Insectes (Pterygota). *Trav. Inst. Paleont. Acad. Sci. URSS* 7. (In Russian with French résumé).

Needham, J. G., J. H. Traver and Yin Chi Hsu. 1935. The biology of mayflies. Ithaca.

Nüesch, H. 1953. The morphology of the thorax of *Telea polyphemus* (Lepidoptera). *Journ. Morph.* 93.

Poletaiew, N. 1881. Du dévelopment des muscles des ailes chez les Odonates. *Horae Soc. Ent. Ross.* 16.

Schwanwitsch, B. N. 1943. Subdivision of Insects Pterygota into Subordinate Groups. *Nature* 152: 727–728.

Schwanwitsch, B. N. 1946. On the interrelations of the Orders of Insecta Pterygota as dependent on the origin of flight. I. *Zool. Journ.* 25 (In Russian with English Summary).

Schwanwitsch, B. N. 1948. II. *Ibid.* 27 (In Russian).

Schwanwitsch, B. N. 1949. A textbook of general entomology. Moscow-Leningrad (In Russian).

Snodgrass, R. E. 1935. Principles of insect morphology. New York.

Tillyard, R. J. 1917. Biology of dragonflies. Cambridge.

Ulrich, W. 1944. Die Mengeiden (Mengellini) und die Phylogenie der Strepsipteren. *Zeit. Paras.* 13.

Voss F. 1913–1914. Vergleichende Untersuchungen über die Flügelwerkzeuge der Insekten. *Verh. Deutsch. Zool. Ges.* 23: 119–142.

Weber, H. 1930. Biologie der Hemipteren. Berlin.

Weber, H. 1933. Lehrbuch der Entomologie. Jena.

Weber, H. 1943. Grundriss der Insektenkunds. Jena.

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Zoologische Staatsinstitut
Hamburg, Germany

Origin and History of the Insect Fauna of the Northern Nearctic

By E. G. Munroe
Entomology Division
Ottawa, Ont.

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[1] Published in the *Proceedings of the Hawaiian Entomological Society* 16 (2): 269-280. 1957.

A Historical Account of Insect Collecting in Northern Canada[1]

By T. N. FREEMAN[2]
Entomology Division
Ottawa, Ont.

ABSTRACT

The paper deals with a historical account of insect collecting in the Canadian arctic and subarctic regions, south of Viscount Melville and Lancaster Sounds, from 1825–1956. The development and extent of the Canadian Northern Insect Survey is included.

This account deals mainly with the collections of insects that have been made from that portion of arctic and subarctic Canada south of Viscount Melville and Lancaster Sounds. The remainder of northern Canada, the Queen Elizabeth Islands to the north, will be dealt with by Mr. P. F. Bruggemann. The insects were obtained from four main sources: (1) the early explorers; (2) individuals associated with mapping and scientific investigations; (3) missionaries; and (4) those concerned primarily with entomological investigations.

EARLY EXPLORERS

The insects collected during these early explorations were obtained by members of expeditions searching for the northwest passage from Europe to the Far East. The hazards and privations of these explorers are well known. The probability of bringing back entomological specimens in good condition was remote. The first noteworthy collection was made in 1825–27 by Dr. J. Richardson, the surgeon attached to the second Sir John Franklin expedition. This expedition was an overland journey from Ft. Chipewyan, Alta., to Great Bear Lake, N.W.T., then to Aklavik, N.W.T., and along the arctic coast to Coppermine, N.W.T. The insects taken by Dr. Richardson were described by Kirby in 1837 in Part 4 of Richardson's Fauna Boreali-Americana.

In 1829–33 Captain J. Ross undertook his second search for the northwest passage and collected insects while icebound during the short summer season off the Boothia Peninsula, in the vicinity of Spence Bay, N.W.T. The insects that were obtained were described by Curtis in 1835 as an appendix to Ross's report. From 1850–55 Captain R. Collinson searched for this passage from west to east, and while icebound during the summer, collected insects on the southern shore of Victoria Island in the vicinity of Cambridge Bay, N.W.T. Actually, very few specimens were obtained by these early explorers.

MAPPING AND SCIENTIFIC INVESTIGATIONS

About the middle of the 19th century it became apparent that the northwest passage to the Orient was impractical, and the period from that time until the present constituted a century of mapping and scientifically investigating the northern portion of Canada. The insects collected up until 1929 were obtained in connection with other primary investigations. In 1860 Robert Kennicott collected insects at Methy Lake, near Ft. McMurray, Alta., while enroute to Alaska to collect biological specimens for the Smithsonian Institution in Washington, D.C. Also in 1860, Dr. A. S. Packard accompanied the Williams College Expedition to Labrador and Greenland and collected for two months along the southern coast of Labrador. He did not go on with the expedition to Greenland. In 1864 he returned to Labrador to secure data to enable him to write a memoir on the geology and natural history of the region, and again he obtained many insects. In 1893, J. B. Tyrrell and his brother J. W. Tyrrell conducted a mapping exploration from Ft. Chipewyan, Alta., to Ft. Churchill, Man., and on to Baker Lake, N.W.T. These men were conducting investigations for the Geological Survey of Canada, and the insects they obtained were subsequently dealt with in the reports of the Canadian Arctic Expedition, which I shall mention later. During the first quarter of the present century a considerable amount of explorative mapping and reconnaissance geology has been undertaken, and a few insects were collected by several individuals associated with this work. Among the most noteworthy were the collections of D. T. Hanbury, who made an overland expedition by dog team and canoe in 1899 from Winnipeg, Man., to Baker Lake, N.W.T., and along the Thelon River to Great Slave Lake, N.W.T. In 1901 he reversed the route from Great Slave Lake to Chesterfield, N.W.T., and in 1902, after wintering with the Eskimos at Baker Lake, went to Coppermine, N.W.T., then to Fort Confidence, Alta., and on to Edmonton, Alta. The Lepidoptera collected by Hanbury were recorded by Elwes in 1903. The next noteworthy collection was made by the Canadian Arctic Expedition in 1913–18. This expedition had the primary purpose of making physical and biological investigations of the territory from Wrangell Island, off the Siberian coast, and along the northern Alaskan and Canadian coasts to Coppermine, N.W.T. Mr. Frits Johannsen, the biologist with the expedition, collected most of the insects. The results of a taxonomic study of these specimens were published by Hewitt *et al.* in volume III, Parts A-K, of the reports of that expedition. The next major entomological collection was made by the Danish Fifth Thule Expedition of 1921–24. This was one of exploration and scientific investigation particularly along archaeological lines. The insects were collected mainly by the party leader, Dr. Knud Rasmussen, a native of Greenland, and Peter Freuchen. The collections that were assembled represented a geographical extension of those obtained by the Canadian Arctic Expedition, and were made mainly from Churchill, Man., to Eskimo Point, N.W.T., along the Kazan River to Baker Lake, and from there to Chesterfield, N.W.T. Some collections were also made from the southern part of the Melville Peninsula and adjacent islands. A few were also obtained from King William and Bylot Islands as well as northern Baffin Island. The insects were recorded by Henriksen in 1937. In 1927 Mr. Johannsen collected a few insects in the region of Hudson Strait. Also in that year Mr. J. D. Soper of the Canadian National Museum at Ottawa collected insects on southern Baffin Island, where he was conducting a mapping reconnaissance and searching for the nesting site of the blue goose. This search for the nesting grounds of the blue goose was also carried on successfully in 1927 by Dr. G. M. Sutton, who collected considerable numbers of insects on Southampton Island in northern Hudson Bay. From 1926 to the present time Mr. A. E. Porsild of the National Herbarium in Ottawa, Ont., has collected insects from time to time in connection with his botanical investigations in various regions across the whole of the Canadian arctic and subarctic regions. In 1929–30 Mr. O. Bryant made collections in the region of Aklavik, N.W.T. Many small lots of specimens have been obtained by various individuals in connection with these mapping and scientific investigations. Perhaps the more important collections are those of I. H. Cox, in 1931, on Akpatok Island in Hudson Strait; J. M. Wordie, in eastern Baffin Island in 1934; A. V. Harper at Churchill, Man., in 1934; and T. H. Manning, a well known explorer and scientist, in various localities throughout the whole of the Canadian Arctic during the past several years.

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[2] Entomologist.

MISSIONARIES

About 150 years ago the Moravian Missions were established along the northern Labrador coast. The missionaries in charge of some of these missions collected insects, some of which were sent to such well known entomologists as Hübner about 1824, and Boisduval about 1829. Much later, from 1930–40, Reverend Perrett collected a considerable amount of insect material at Hopedale, Labrador. Also at that time, Reverend Turner made important collections in northern Baffin Island.

In 1892 Dr. W. T. Grenfell founded the Grenfell Medical Mission at St. Anthony, Nfld. Since that time these missions have been established on the southern coast of Labrador, and as a result, many substantial contributions have been made to our knowledge of the insect fauna of that region.

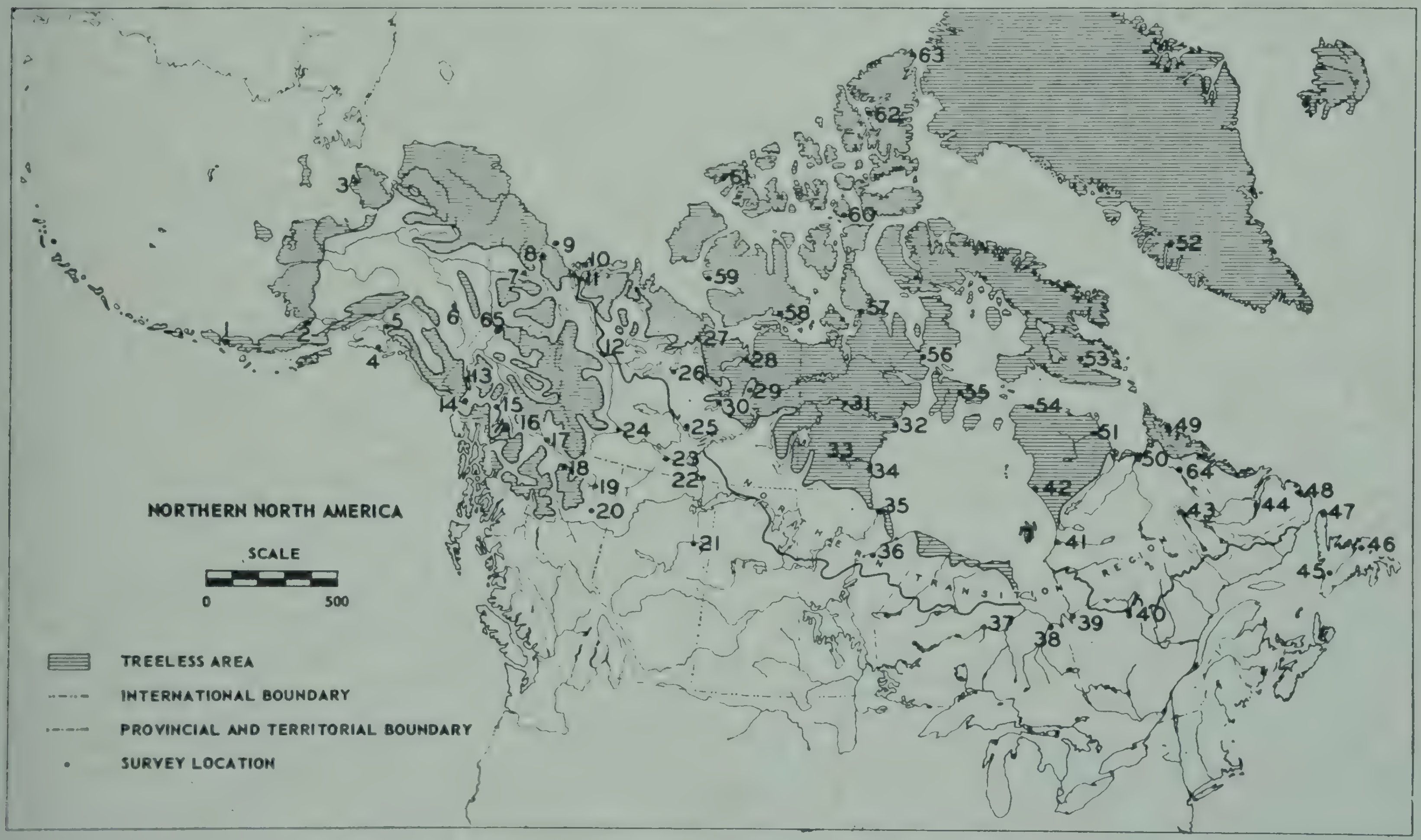
ENTOMOLOGICAL INVESTIGATIONS

It will be noted that all of the collections previously mentioned were made in connection with other investigations and it was not until 1929–30 that Mr. W. J. Brown of the Division of Entomology, Canada Department of Agriculture, conducted the first investigation for entomological purposes only, along the north shore of the Gulf of St. Lawrence. This was followed by other entomological surveys by officers of the Division of Entomology at Ottawa as follows: Mr. G. S. Walley, to Smoky Falls and Moosonee, Ont., in 1934;

Mr. W. J. Brown, in southern Baffin Island in 1934, and at Churchill, Man., in 1937; also in 1937 T. N. Freeman collected at Great Bear Lake, N.W.T.

In 1947 the Defence Research Board of the Canadian Department of National Defence requested the Entomology Division, Science Service, Canada Department of Agriculture, to study biting flies and other entomological problems of the Canadian arctic and subarctic regions. This was the first major organized project of entomological research in northern Canada. The research program was divided into three major phases as follows: (1) investigations on life histories, habits, ecology, and control of biting flies by the Veterinary and Medical Entomology Unit, directed by Dr. C. R. Twinn; (2) The Northern Insect Survey, which deals with systematics, distribution, relative abundance, and ecology of biting flies and other insects, directed by the Insect Systematics and Biological Control Unit, assisted by the Botany Unit, and co-ordinated by the writer; (3) investigations on laboratory rearing techniques for northern mosquitoes, and on behaviour and systematics of certain mosquito species of the genus *Aedes*, by the Defence Research Board at the Defence Research Northern Laboratory, Fort Churchill, Manitoba, conducted by Dr. W. E. Beckel.

The Canadian Northern Insect Survey started in 1947 by my own studies and collections made in the vicinity of Churchill, Man., and Baker Lake, N.W.T. Since that time sixty expeditions have been sent into the arctic and subarctic regions as shown on the accompanying map. The area we have attempted to investigate is very large. The northernmost investigations were made at Alert in northern Ellesmere Island. This locality is approximately 2500 miles or 3500 km. north of Montreal, about 500 miles from the geographical north pole, and many miles north of the magnetic pole. The distances east to



1, Cold Bay, Alaska; 2, Naknek, Alaska; 3, Nome, Alaska; 4, Seward, Alaska; 5. Anchorage, Alaska; 6, Big Delta, Alaska; 7, Rampart House, Yukon; 8, Firth River, Yukon; 9, Herschel Island, Yukon; 10, Kidluit Bay, N.W.T.; 11, Reindeer Depot, N.W.T.; 12, Norman Wells, N.W.T.; 13, Burwash Landing, Yukon; 14, Haines Cut-Off, Yukon; 15, Whitehorse, Yukon; 16, Atlin Lake, B.C.; 17, Watson Lake, Yukon; 18, Muncho Lake, B.C.; 19, Fort Nelson, B.C.; 20, Mason Creek, B.C.; (13–15, 17–20, Alaska Highway Expedition); 21, Fort McMurray, Alta.; 22, Fort Smith, N.W.T.; 23, Hay River, N.W.T.; 24, Fort Simpson, N.W.T.; 25, Yellowknife, N.W.T.; 26, Saw Mill Bay, N.W.T.; 27, Coppermine, N.W.T.; 28, Bathurst Inlet, N.W.T.; 29, Muskox Lake, N.W.T.; 30, MacKay Lake, N.W.T.; 31, Baker Lake, N.W.T.; 32, Chesterfield, N.W.T.; 33, Padlei, N.W.T., 34, Eskimo Point, N.W.T.; 35, Churchill, Man.; 36, Gillam, Man.; 37, Ogoki Post, Ont.; 38, Moosonee, Ont.; 39, Rupert House, Que.; 40, Mistassini Post, Que.; 41, Great Whale River, Que.; 42, Port Harrison, Que.; 43, Knob Lake, Que.; 44, Goose Bay, Nfld.; 45, Harmon Field, Nfld.; 46, Gander, Nfld.; 47, St. Anthony, Nfld.; 48, Cartwright, Nfld.; 49, Hebron, Nfld.; 50, Fort Chimo, Que.; 51, Payne Bay, Que.; 52, Sondrestrom Fiord, Greenland; 53, Frobisher Bay, N.W.T.; 54, Sugluk, Que.; 55, Coral Harbor, N.W.T.; 56, Repulse Bay, N.W.T.; 57, Spence Bay, N.W.T.; 58, Cambridge Bay, N.W.T.; 59, Holman Island, N.W.T.; 60, Resolute Bay, N.W.T.; 61, Mould Bay, N.W.T.; 62, Eureka, N.W.T.; 63, Alert, N.W.T.; 64, Indian House Lake, Que.

west covered by the Survey are even greater, from Nome, Alaska to Sondrestrom Fiord, Greenland.

Following is a chronological résumé of the number of expeditions, stationed each year for the duration of the collecting season, at the 60 localities that were investigated in this vast area:

1947— 1 expedition
1948— 8 "
1949—11 "
1950— 8 "
1951—12 "
1952—7 expeditions
1953—4 "
1954—5 "
1955—2 "
1956—2 "

In addition to the objectives of the Survey as previously mentioned, representative collections were made of insects in all orders. It is almost impossible to state exactly the number of specimens that have been obtained; perhaps a quarter of a million would be a fair estimate. Some of the more recent results of the Survey will be presented later in this symposium. A list of references to earlier work is contained in a paper by Freeman in 1955. It will be many years before all the insects that have been obtained will be taxonomically studied. To make it possible to obtain this huge collection of insects, made difficult by the lack of regular transportation and accommodation, many organizations have considerably assisted with this task. I should like to acknowledge the many favors received from the Defence Research Board; the Royal Canadian Air Force; the United States Air Force; many factors of the Hudson's Bay Company posts established throughout the north; the Moravian and Grenfell Medical Missionaries; the Meteorological Division of the Department of Transport, the Department of Northern Affairs and National Resources; the Royal Canadian Mounted Police; and the Department of National Health and Welfare; without whose co-operation the Canadian Northern Insect Survey would not have obtained the degree of success it has reached.

REFERENCES

Blair, K. G. 1933. Coleoptera collected by the Oxford University Expedition to Akpatok Island, Ungava Bay, Aug.-Sept., 1931. *Ann. Mag. Nat. Hist.* 12: 93–96.

Curtis, J. 1835. Appendix to the narrative of a second voyage in search of the northwest passage by Sir John Ross. London, pp. lix-lxxx.

Elwes, H. J. 1903. On a collection of Lepidoptera from arctic America. *Trans. Ent. Sec. London*: 239–244.

Freeman, T. N. 1955. Present trends and future needs of entomological research in northern Canada. Part 1. The northern insect survey. *Arctic* 5: 175–177.

Harrington, W. H. 1890. On the lists of Coleoptera published in the reports of the Geological Survey of Canada from 1842–1888. *Canad. Ent.* 22: 184–191.

Hewitt, C. G., *et al.* 1922. Report of the Canadian Arctic Expedition, 1913–18. Vol. 3: Insects. Ottawa, *King's Printer*, Parts A to L.

Henriksen, K. L. 1937. Insects collected on the Fifth Thule Expedition. *Rept. Fifth Thule Exped.* 1921–24, Vol. 2, Zoology, No. 8: 34 pp.

Kirby, W. 1837. The insects. Part 4 *in* Fauna Boreali-Americana by Sir J. Richardson *et al.*, 1829–37. London, 325 pp.

Longstaff, T. G. 1936. Entomological note on Mr. T. M. Wordie's expedition to N. W. Greenland and E. Baffinland in 1934. *Ann. Mag. Nat. Hist., Ser.* 10, 15: 531–533.

Packard, A. S. 1867. View of the lepidopterous fauna of Labrador. *Proc. Boston Soc. Nat. Hist.* 5: 32–63.

Packard, A. S. 1870. List of coleoptera collected by A. S. Packard, Jr., at Caribou Island, Labrador, Straits of Belle Isle. *Canad. Ent.* 2: 119.

Packard, A. S. 1872. List of the Coleoptera collected in Labrador. *Fourth Ann. Rept. Trustees Peab. Acad. Sci.* pp. 92–94.

DISCUSSION

G. J. Kerrich. How fortunate we are to have this introduction to the symposium. Those who have seen something of the European Arctic and Subarctic must have been struck by the similarities.

R. I. Sailer. What attempts have been made to revisit localities and to correlate differences in the fauna with meteorological data?

T. N. Freeman. Coral Harbour on Southampton Island and Eureka Sound on Ellesmere Island have each been investigated twice. Except for some general meteorological correlations with mosquito abundance no serious work of this nature has been undertaken by the Northern Insect Survey.

Harry K. Clench. How long is it proposed to continue the Northern Insect Survey?

T. N. Freeman. The Northern Insect Survey will probably be continued for several years at a reduced tempo; possibly one or two parties each year. One of the difficulties is to find an established base from which to work. We have visited most of the existing settlements.

Distribution Patterns of the Scatomyzinae (Diptera, Muscidae)[1]

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ABSTRACT

The Scatomyzinae are almost entirely north temperate and arctic. The distribution of the Canadian species (except that of the arctic species) does not correspond well with the boundaries of the formal faunal zones; instead four main distributional types are suggested. The arctic zone is very distinct; not only almost all the species, but many of the subgenera and genera as well, are endemic; this indicates a long adaptation of the groups to arctic conditions. The distribution of the few Greenland species suggests that the island may be divisible into a northern arctic and a southwestern (or southern?) faunal zone. Tentative conclusions concerning the area of proliferation of three of the larger genera are presented. The distribution within North America and Eurasia of the Holarctic species, and particularly the distribution of the species occurring in Greenland, suggests that, with the exception of two littoral species, all interchange of Scatomyzinae between the Nearctic and Palaearctic regions has probably been by way of Bering Strait, and that the Scatomyzine fauna of Greenland is in large part of Nearctic origin.

The Diptera of the subfamily Scatomyzinae (=Cordilurinae, Scatophaginae) are almost entirely north temperate and arctic in distribution. Excluding the genus *Amaurosoma*, which has not been fully studied, 257 species are known to me. In the New World they occur throughout North America south to the highlands of Southern Mexico; in the Old World, south to North Africa, the south slopes of the Himalaya, the Burma-China border and Formosa. South of these regions they have been found only in Haiti, the high Andes, the mountains of East Africa, the Cape of Good Hope and St. Helena. All six of the southern hemisphere forms belong to the very large genus *Scatophaga;* with the possible exception of *Scatophaga stercoraria* (L.), which occurs as a distinct subspecies in East and South Africa and St. Helena, and has three other close relatives in East Africa, the southern hemisphere has apparently contributed nothing to the northern fauna. All the forms occurring along the southern border of the main area of distribution belong to northern genera.

Little is known of larval habitats. The known larvae of the 20 species of Cleigastrini, one of the two tribes, are all leaf-miners in species of the monocotyledonous families Liliaceae, Orchidaceae and Commelinaceae. The few known larvae of the species of Scatomyzini have very diverse habits—they occur in dung, in rotten seaweed, boggy soil, sewage beds, rapidly flowing rivers, and in various parts of a variety of plants (*Scirpus, Rumex, Nuphar, Pedicularis*). Except for two species apparently confined to water lilies, and six littoral species, two of which (and probably all) occur as larvae in decaying seaweed, too little is known of the requirements of larvae or adults of any species to attempt to account from their distribution on these grounds. Nothing but bare records of geographic distribution (and most of these from Europe and North America) have been available for most species.

Using a slightly modified version of the map of North American faunal zones published by Muesebeck, Krombein and Townes (1951), an analysis of the distribution of 92 Canadian species was undertaken. Littoral species, and species for which less than four locality records were available, were excluded, unless a smaller number of records indicated occurrence in two or more faunal zones. The modifications in the map were a northward extension of the Eastern Transition Zone to include the area on both sides of Lake Superior west to Central Manitoba and east to include a narrow area along the north shore of the St. Lawrence River to Quebec City, the Gaspe Peninsula, the Maritime provinces of Canada and northern New England, and a narrow extension of the Canadian zone along the north shore of the Gulf of St. Lawrence almost to the Labrador boundary. Also, the eastern and western portions of the Transition Zone were treated as distinct as suggested by Kendleigh (1954), rather than as sub-divisions of a single zone. The results are shown in Table I.

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[2] Entomologist.

TABLE I.—Distribution of Canadian Scatomyzinae within Faunal Zones.

	Occurring in	Restricted to
Arctic	21	18
Hudsonian	38	7
Canadian	43	0
Eastern Transition	43	3
Western Transition	35	8
Upper Austral	12	0

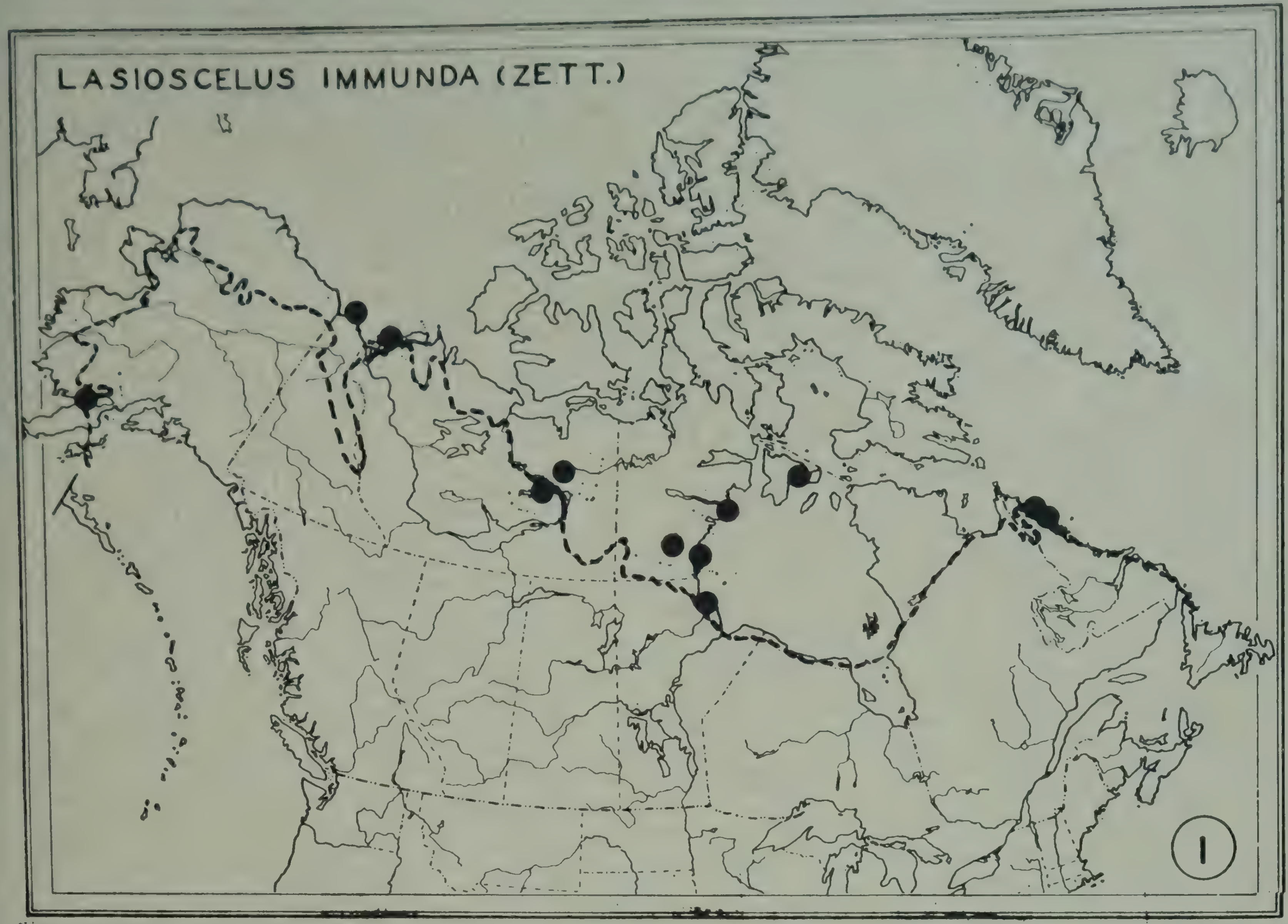
Of the 92 species, 36 occur in only one faunal zone, 32 in two, 12 in three and 13 in four or more. The most striking fact is the high degree of endemism of the arctic species. Although the limit of trees is not sharply defined, and in a number of localities at or near treeline both Arctic and Hudsonian species are known to occur, evidence from the Scatomyzinae indicates that no other zonal boundary in Canada even approximates this one in definition. Distributions of some of the more abundant arctic species are shown in Figs. 1–4.

In most groups of Diptera, and, according to a verbal communication from Dr. W. R. M. Mason, in the Hymenoptera as well, few endemic arctic genera or subgenera occur; most of the arctic species belong to subarctic or to widespread genera. In the Scatomyzinae, however, of the 18 endemic species, only four belong to genera or subgenera occurring outside the arctic; eight belong to four endemic genera and six more to three endemic subgenera. This indicates an extremely long adaptation of the group to arctic conditions and a considerable proliferation within the arctic (one arctic genus has four species in North America with two more in the Old World arctic).

Although, apart from the arctic ones, few species fit well into Merriam faunal zones, the distributions in conjunction with the abundance of records in the various zones suggest four main distribution types for North American Scatomyzinae. These are (1) an arctic transcontinental on the tundra, (2) a boreal transcontinental (Hudsonian and Canadian zones) in the coniferous forest region, with a small number of species restricted to the northwest or the Cordillera but none to the eastern half of North America, (3) an eastern (Eastern Transition and Upper Austral zones) in the deciduous forest region, and (4) a western (Western Transition zone) with some species restricted to the Cordillera but with many extending across the great plains to the western edge of the eastern forest.

It is possible that if population figures were known for many species the traditional faunal zones, outlined in greater detail to include obvious enclaves of one zone within another or extensions of one zone into another would indicate in most cases the actual range of a species. Many species abundant in one zone occur outside the zone only in very small numbers. Also, predominantly Hudsonian and Canadian zone species of many groups occur south of these zones in bogs, where their occurrence can often be predicted, although small scale faunal zone maps give no hint of it.

Greenland is treeless and superficially resembles the arctic zone of the rest of North America (with which it is included in the Muesebeck and Krombein map). Seven species of Scatomyzinae have been recorded from Greenland (Henriksen, 1939). One species, *Scatophaga stercoraria* (L.), normally common where it occurs, has been recorded only once; the record is very probably based on a misdetermination. Two species, *Scatophaga furcata* (Say) and *Scatophaga litorea* (Fall.), occur in the rest of North America in both the arctic and subarctic. The other four species occur in the rest of North America in either the arctic or the subarctic; their distribution is shown in Figs. 3–5. The three arctic species are known only from the northern half of Greenland; the one subarctic species, *Microproposa haemorrhoidalis* (Mg.), has been taken only in the southern part of Greenland



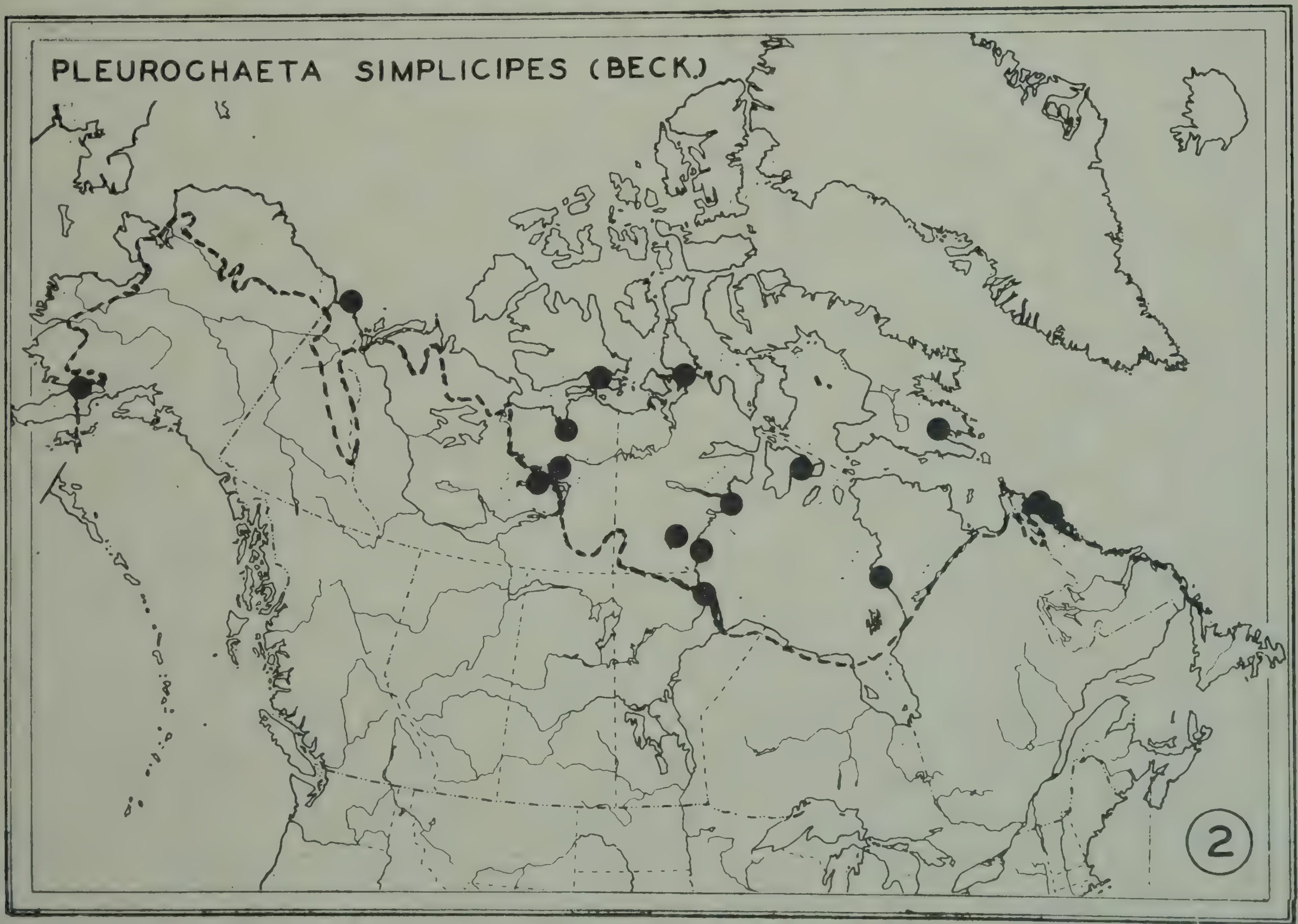
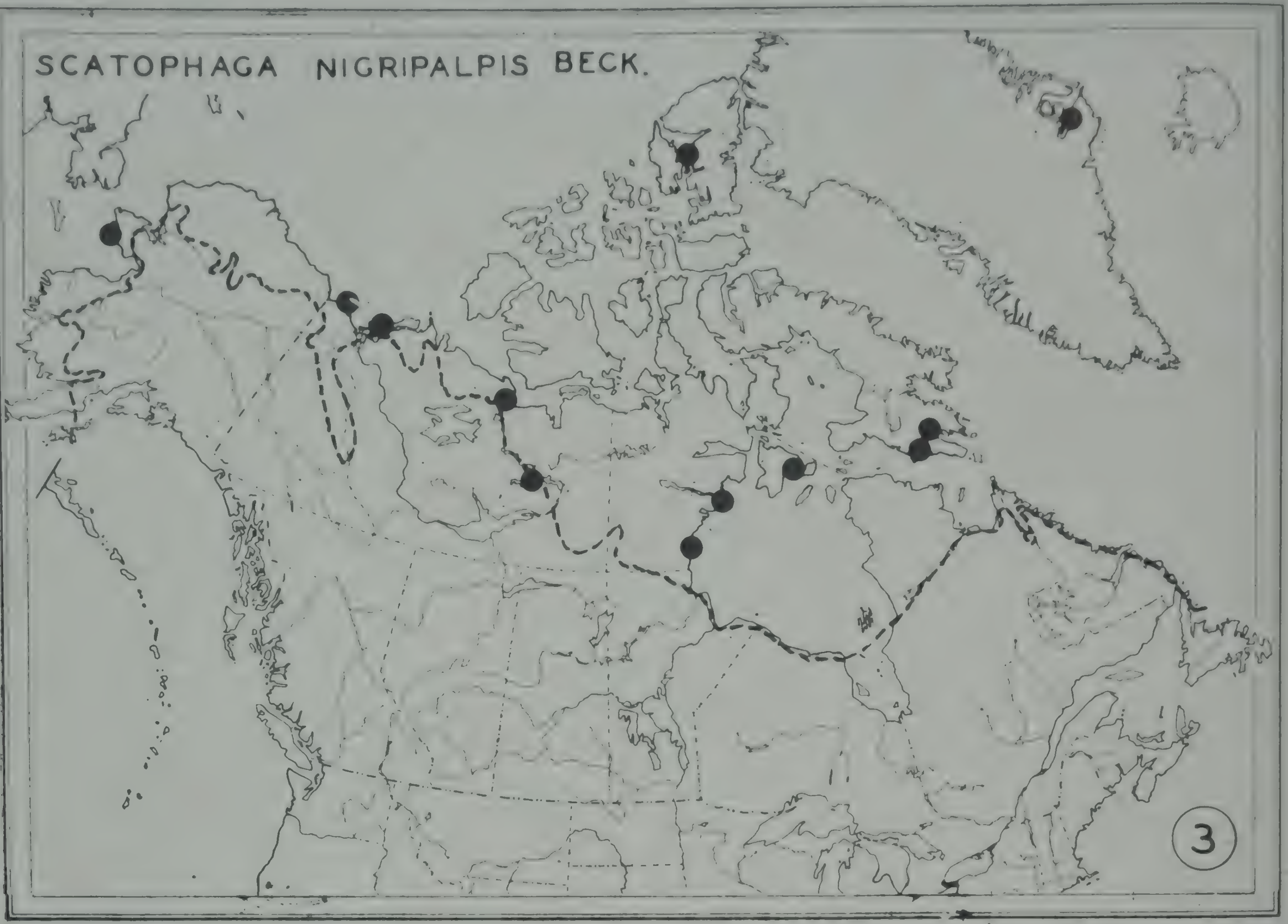


Fig. 1. The distribution of *Lasioscelus immunda* (Zett.) in North America. The broken black line in this and succeeding maps indicates the northern limit of trees. Fig. 2. The distribution of *Pleurochaeta simplicipes* (Beck.) in North America.

where it is apparently abundant. Whether the division of Greenland into a northern arctic and a southwestern (or southern?) subarctic zone is actually as distinct as the known distribution of these four species suggests I do not know, although records of a few other

Diptera indicate that it may be. More comparisons of Greenland with forms from the rest of North America will be necessary to determine this.

Most of the genera are too small or too evenly distributed between the Palaearctic and Nearctic for any indication of their place of development and proliferation to remain.



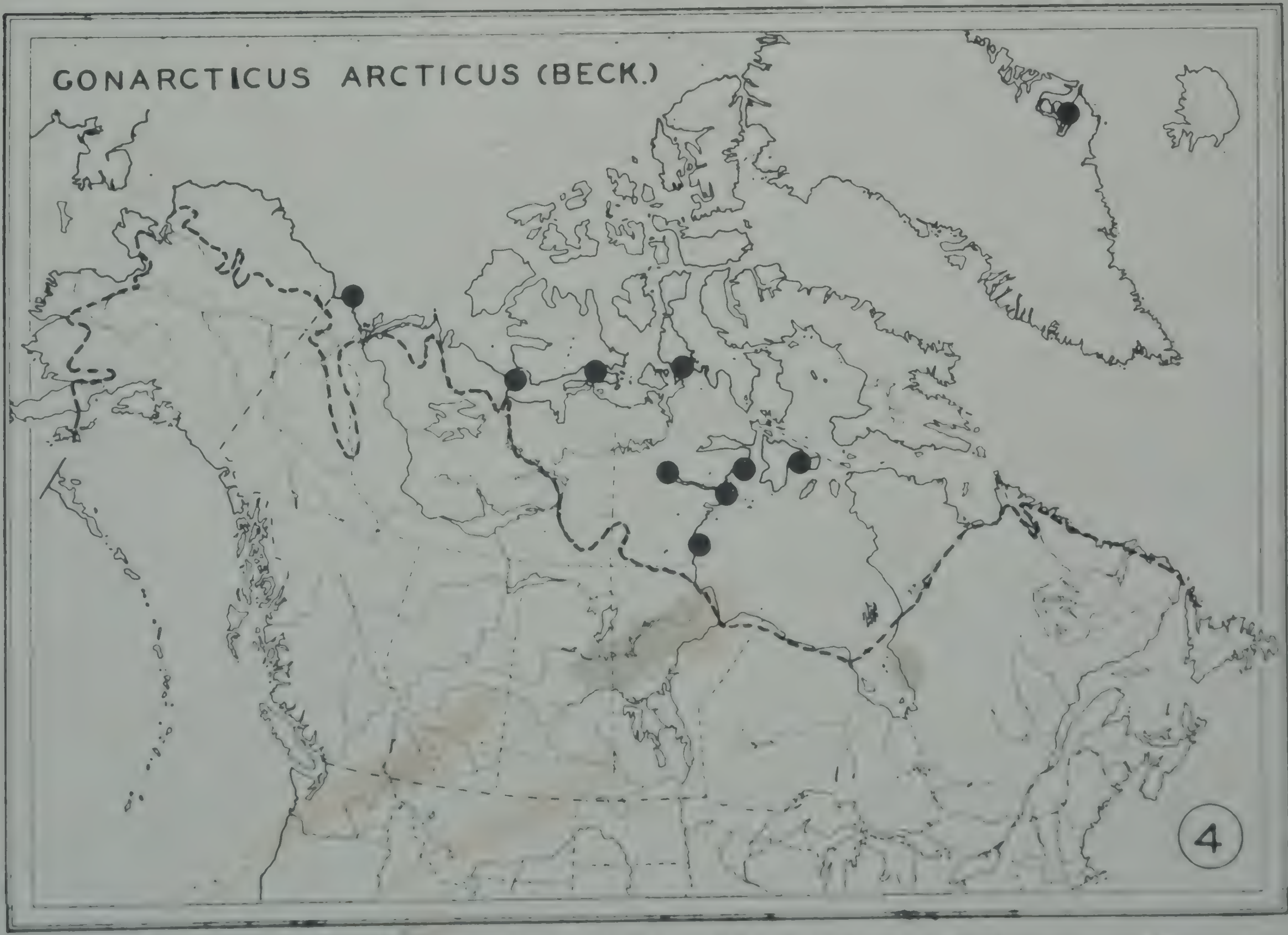
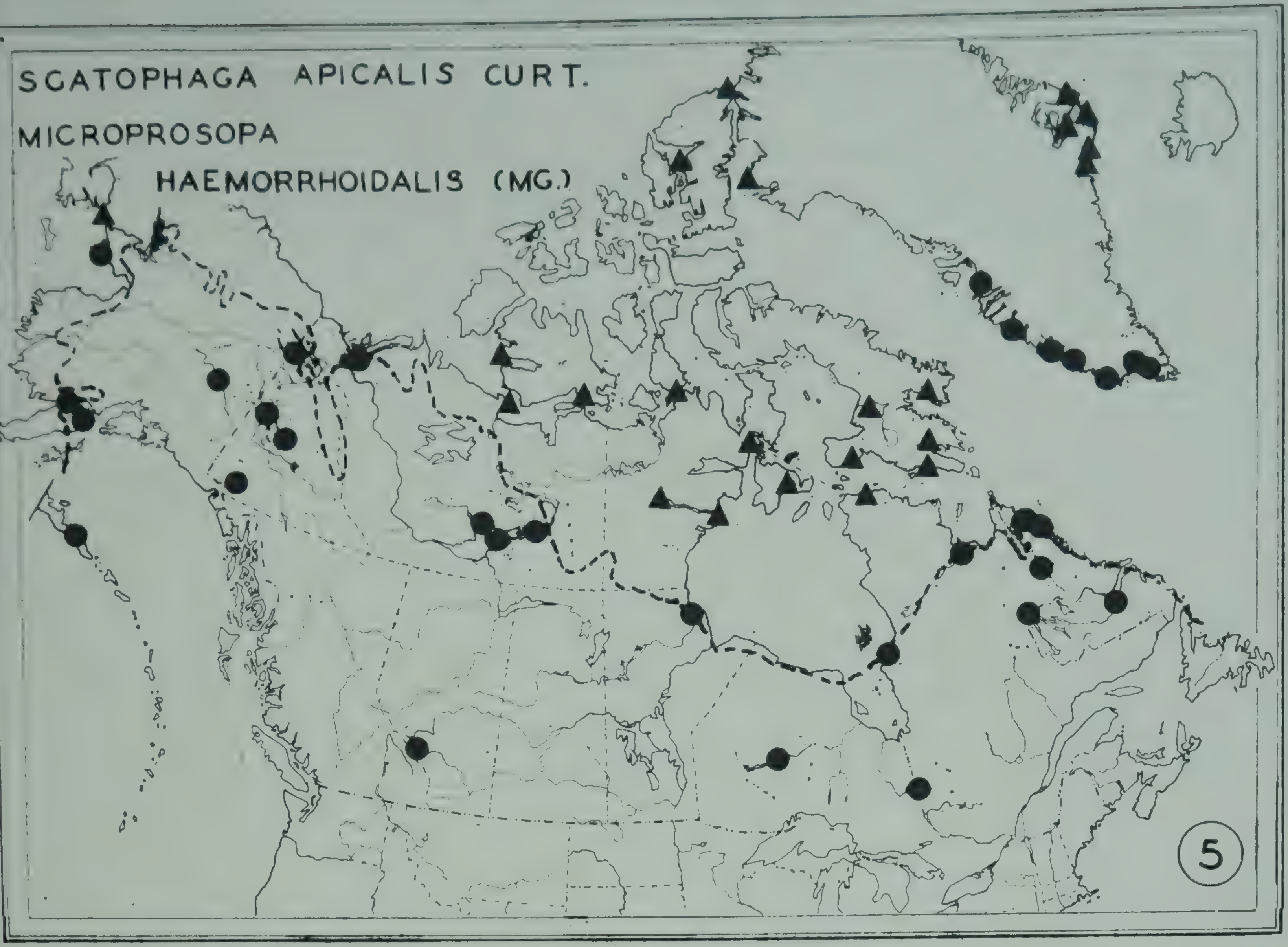


Fig. 3. The distribution of *Scatophaga nigripalpis* Beck. in North America. Fig. 4. The distribution of *Gonarcticus arcticus* (Beck.) (described as *Pselaphephila arctica* Beck.) in North America.


SCATOPHAGA APICALIS CURT.
MICROPROSOPA
HAEMORRHOIDALIS (MG.)
5

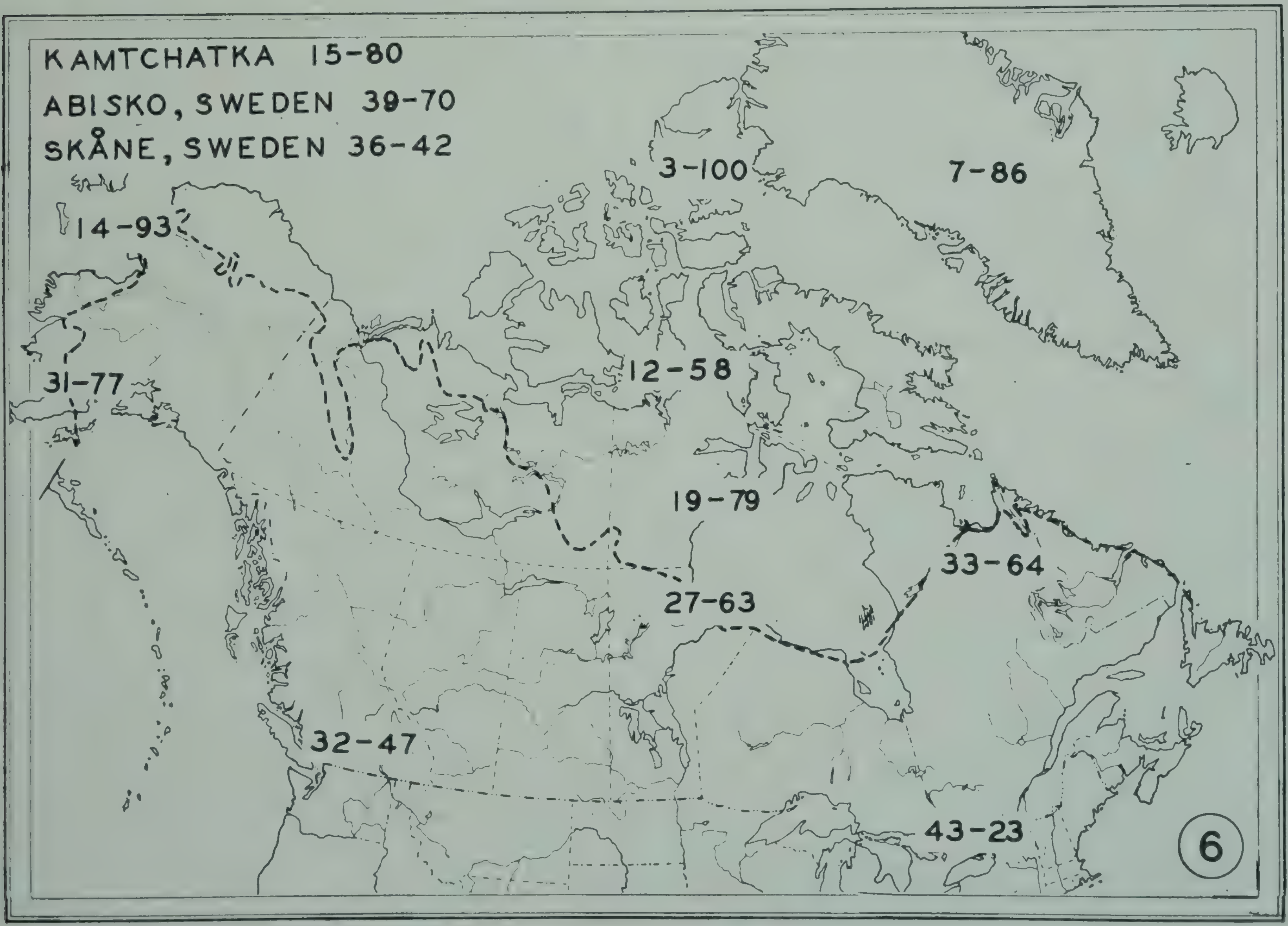

KAMTCHATKA 15-80
ABISKO, SWEDEN 39-70
SKÅNE, SWEDEN 36-42
3-100
7-86
14-93
31-77
12-58
19-79
33-64
27-63
32-47
43-23
6

Fig. 5. The distribution of *Microprosopa haemorrhoidalis* (Mg.) [●] and of *Scatophaga apicalis* Curt. [▲] in North America. Fig. 6. Number of species of Scatomyzinae (first figure) and percentage of species which are Holarctic (second figure) for each of a number of localities or areas in North America and Eurasia.

For three genera, however, a tentative conclusion is possible. *Norellia* has 14 old world species; most of these are known only from central and southern Europe. Only one, and that the commonest and most northern of the European species, is known from North America. It is almost certainly a recent immigrant. *Cordilura* has 41 Nearctic, 15 Palaearctic and seven Holarctic species. In Europe the genus is northern; none of the species is restricted to southern or central Europe; 16 of 22 species occur in Finland (Hackmann, 1956), and of these only four are southern in distribution, three are widespread and nine are predominantly northern within Finland. In North America only 13 of the 48 species are of the boreal transcontinental type; the rest are centred in the eastern or western regions mentioned above, except for one known only from Central Mexico. This indicates a predominantly New World development with more than one period of faunal interchange; some of the European species are rather distinct. For *Scatophaga* the evidence is less decisive. The New World has almost as many species as the old, but there they are mostly northern or western; only one species is restricted to eastern North America. In the Palaearctic the species appear to be rather evenly distributed, with many more in Europe than in eastern North America. The genus seems to be largely old world in development, but one of the Mexican species and the single South American species are quite distinct; the first movement of the group into North America must have been very ancient.

The only other large genus, *Gimnomera*, has a very peculiar distribution. The eight Palaearctic species are arctic, boreal or alpine, as are at least 10 of the 13 Nearctic species, and each of the two main species groups is represented in each region. However, not one of the species is Holarctic. With this exception, only a few small or southern genera are without Holarctic species.

The possible regions of mass faunal interchange between North America and Eurasia have almost certainly been at most two—the Bering Strait region and the North Atlantic region. Of 257 species of Scatomyzinae, 45, or 17%, are Holarctic. The Holarctic species are not, however, evenly distributed over North America. The number of species, and the percentage of Holarctic species in several parts of North America are shown in Fig. 6. The localities or areas are Eureka, Ellesmere I. (3,100%); Greenland (7,86%, or, if the doubtful species mentioned above is disregarded, 6,83%); Spence Bay, N.W.T. (12,58%); Chesterfield Inlet, N.W.T. (19,79%); northern third of Quebec (33,64%); Ottawa, Ont., district (43,23%); Nome, Alaska (14,93%); Naknek and King Salmon, Alaska (31,77%); Churchill, Man. (27,63%); southern third of British Columbia (32,47%). Figures are also available for three parts of the Palaearctic—Kamtchatka, Siberia (15,80%); Abisko National Park, Lapland, Sweden (39,70%); Skane, southern Sweden (36,42%).

The proportion of Holarctic species in both continents increases generally northward and toward Bering Strait; this strongly suggests that most of the faunal interchange occurred there. The percentage for Greenland and Ellesmere I. are high, suggesting possible transatlantic movement, but the number of species is low and the sampling error may be high.

The Greenland species may be considered individually. Of the seven, three (including the doubtful one) are widespread species occurring across North America, in Iceland and in Europe. The other four species (three and possibly all are Holarctic) are unknown from Iceland and the other North Atlantic Islands, but all occur in northeastern Canada and it seems probable that they have entered Greenland from this direction rather than from Europe.

A littoral species, *Ceratinostoma ostiorum* (Curtis), is known only from the European and North American Atlantic coasts, and has probably crossed the Atlantic; it is unknown from Greenland and Iceland and its route is doubtful. Another littoral species, *Scatophaga litorea* (Fall.), is widespread on North Atlantic mainland and island coasts (including the coast of Greenland), and has almost certainly crossed the Atlantic. With these two exceptions no eastern North American species have close European affinities; interchange of Scatomyzinae between Nearctic and Palaearctic seems to have been almost entirely via Bering Strait.

REFERENCES

Hackmann, W. 1956. The Scatophagidae (Dipt.) of Eastern Fennoscandia. *Soc. Pro Fauna Flora Fenn., Fauna Fenn.* II: 1–67.

Henriksen, K. L. 1939. A revised index of the insects of Greenland. *Meddelelser om Grønland* 119 (10): 1–112.

Kendleigh, S. C. 1954. History and evaluation of various concepts of plant and animal communities in North America. *Ecology* 35: 152–171.

Muesebeck, C. F. W., K. V. Krombein and H. K. Townes. 1951. Hymenoptera of America north of Mexico—Synoptic Catalog. *U.S. Dept. Agric., Agric. Monog. No. 2.*

DISCUSSION

F. I. VAN EMDEN. It appears that you consider the family as undoubtedly monophyletic. According to the facts shown by you it cannot have originated in the Southern Hemisphere. Is there any evidence to show that the Scatophagidae first evolved in one of the two components of the Northern Hemisphere, i.e. the Old or the New World?

J. R. VOCKEROTH. The group as a whole, and, with the exception of the three genera (*Scatophaga*, *Cordilura*, *Norellia*) discussed above, most of the genera are rather evenly distributed throughout Holarctica; I know of no evidence to indicate that the group first evolved in the Old World rather than the New, or vice versa.

C. B. PHILIP. The evidence of holarctic interchange not only across the Bering Sea, but in a few instances across the North Atlantic is also observed in the few Tabanidae that are known to be holarctic. *Hybomitra flavipes* is an example known on each side of the Atlantic, that does *not* occur across boreal Canada into Alaska.

R. I. SAILER. By comparison with Dr. Vockeroth's data for Scatomyzidae it might be of interest that 1/3 of the 120 Alaskan species of Heteroptera are Holarctic in distribution.

GEO. STEYSKAL. Sciomyzidae of Alaska are 50%, possibly more, Holarctic.

Ecology of Arctic and Subarctic Mosquitoes

By Dale W. Jenkins
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ABSTRACT

Distributional and ecological data have been compiled for 38 species of mosquitoes occurring in the arctic tundra and subarctic conifer forest regions of the world. The distributions correlate well with various major plant communities, or with specific ecological habitats. Of the 38 species of mosquitoes 32 occur in North America and 23 in Eurasia, and 19 in both continents. In the Rocky Mountains of western North America there is a close correlation between elevation of occurrence of the mosquitoes and latitude. The reasons for the abundance of mosquitoes in the northern areas are abundance of breeding places and nutritive material, lack of competition or severe predation and parasitism, and the short but intense growing season. These factors combined with the adaptations of the mosquitoes enabling them to exploit these conditions result in large populations which are very difficult to control.

INTRODUCTION

The northern land mass of the world consists of a vast cold treeless area known as the tundra. This area is inhabited by a limited number of species of plants and animals characterized in general by their ability to exist in spite of extreme cold winters and a short summer season, and by their wide northern distribution. Immediately south of the tundra lies an enormous subarctic coniferous forest extending in a wide band across North America and Eurasia. This area is commonly called the taiga or muskeg and is characterized by spruce and fir trees, reindeer and sphagnum mosses, and many heath plants. The plants and animals are usually wide ranging and holarctic in distribution. These two regions in North America and Eurasia are shown in Figs. 1 and 2.

Mosquitoes and other biting insects occur throughout these areas in enormous numbers and their abundance and ferocious habits are vividly documented in reports of explorers and inhabitants. Mosquitoes have been reported to be such bad pests that certain regions were considered uninhabitable and progress in development was halted.

The arctic and subarctic regions constitute a last frontier, in which expansion is taking place. It is therefor essential to learn everything possible about the ecology and distribution of these mosquitoes to permit effective control. Until recently little was known about northern mosquitoes except for fragmentary data and collections from expeditions.

In North America intensive study was begun in 1947 in Alaska by the Alaska Insect Control Project under the direction of the U.S. Department of Agriculture, and in northern Canada by the Northern Insect Survey and the Arctic Insect Biology and Control Group under the direction of the Canadian Department of Agriculture. Both programs were sponsored by their respective Departments of Defence.

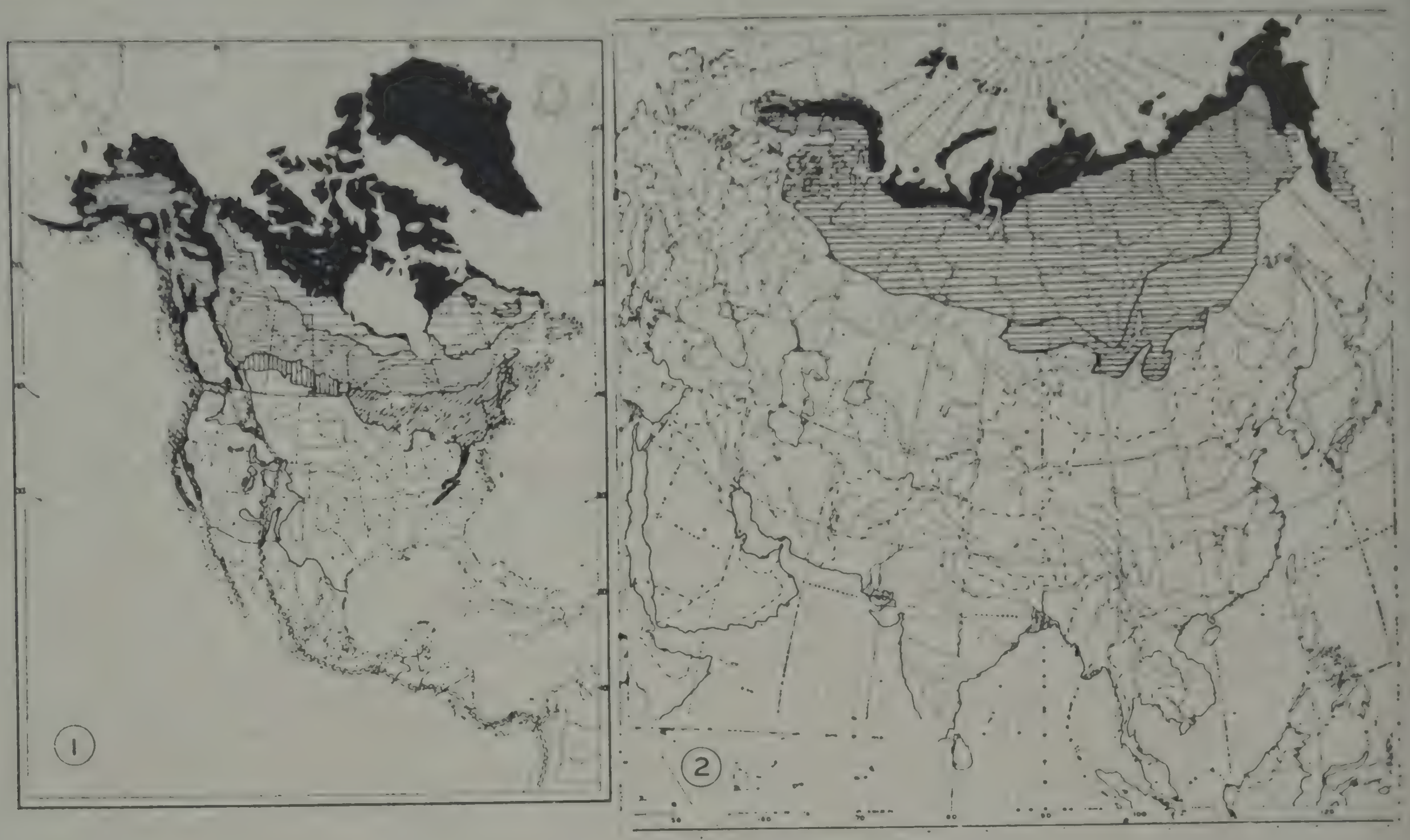
Ecological and distribution data on the arctic and subarctic mosquitoes have been compiled from all available literature, and from studies by the present author working with the above groups during five seasons in Alaska and the Aleutians, in Canada at Churchill, James Bay, Southampton Island, and eastern Hudson Bay, and in the United States in the Rocky and Appalachian Mountains.

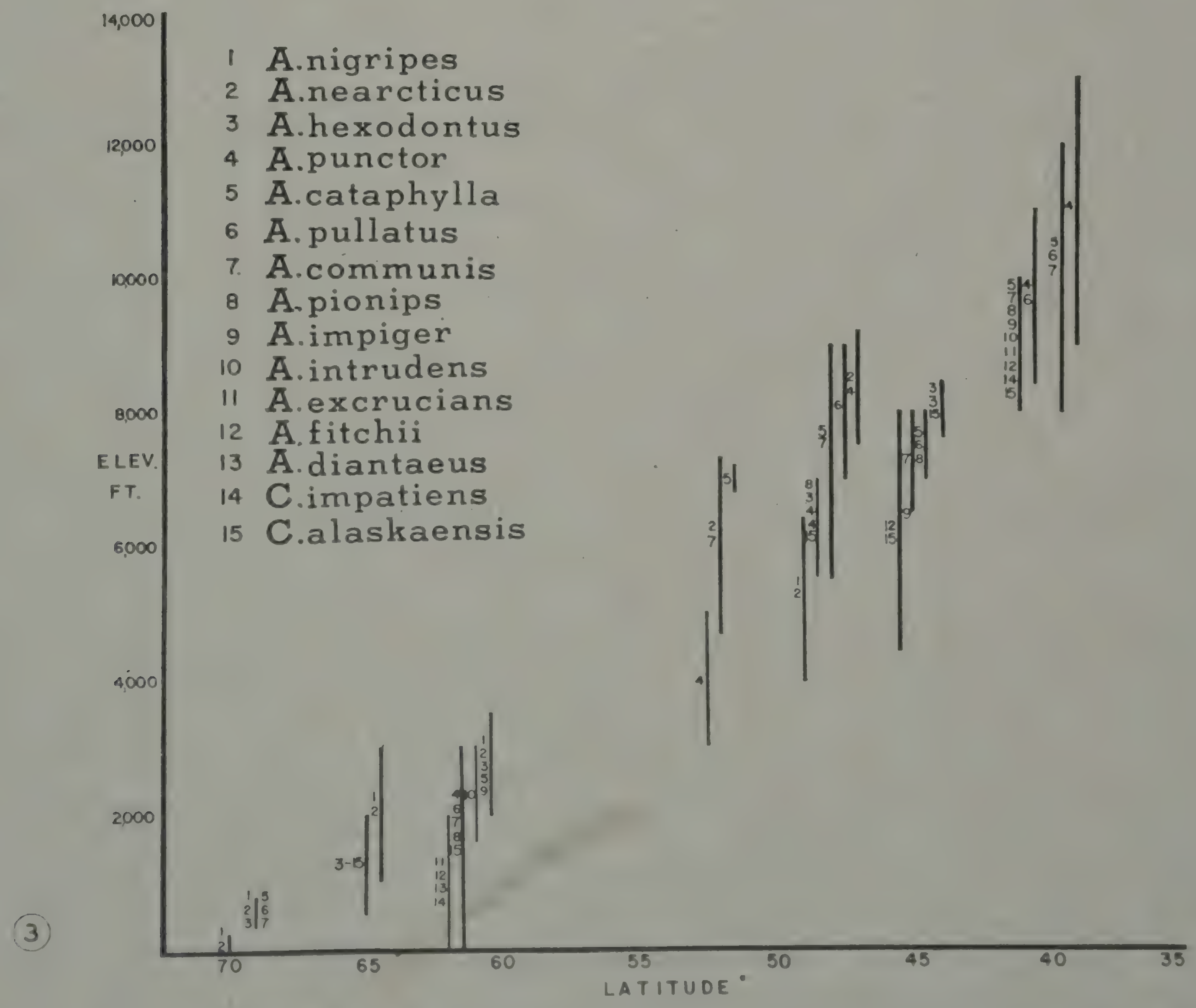
In Eurasia an excellent monograph by Natvig, 1948, critically summarizes all mosquito data for Fennoscandia and surrounding areas. Except for many local studies on the northern Asiatic mosquitoes no general publication has appeared since the book on the Mosquitoes of Russia by Stackelberg in 1937.

In this paper the distribution of the arctic and subarctic mosquitoes of the world are presented and the mosquito fauna of the old and new worlds are compared. Distribution maps of each species are correlated with ecological climax communities, and the effects of past and present climatic conditions are discussed in relation to present distribution. The relative abundance, dispersal habits, and other factors correlating with distribution are presented.

THE ARCTIC AND SUBARCTIC MOSQUITOES

In the arctic and subarctic regions of the world there are 38 described species of mosquitoes as shown in Table I, of which 28 species are in the genus *Aedes*, 6 in *Culiseta*,





Figs. 1, 2. Distribution of arctic tundra (in black) and subarctic coniferous forest or muskeg or taiga (lined area). 1, North America. 2, Eurasia.

Fig. 3. Relations between elevation of occurrence of arctic and subarctic mosquitoes and the latitude in western North America. (2. *A. nearticus* is now *A. impiger*, and 9. *A. impiger* is *A. implicatus*).

2 in *Culex* and 2 in *Anopheles*. Of the *Aedes*, 26 species belong to the *Ochlerotatus* subgenus and include the majority of the worst pest mosquitoes.

TABLE I—Arctic and Subarctic Mosquitoes.

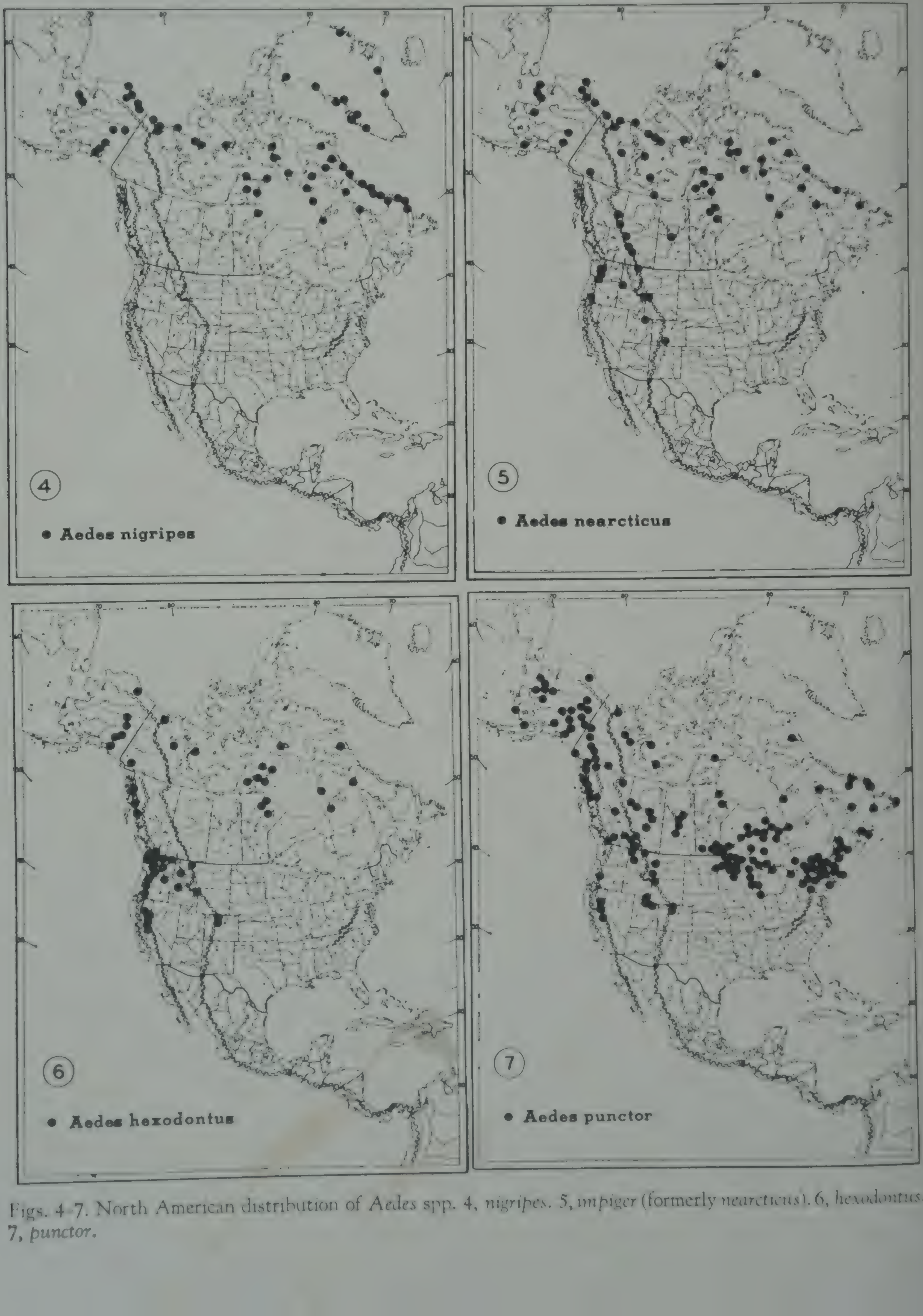
Species		Local or Rare	North America	Eurasia
1. Aedes aboriginis		L	X	?
2. abserratus		L	X	
3. campestris			X	
4. canadensis			X	
5. cantans				X
6. cataphylla	Alpine		X	X
7. cinereus			X	X
8. communis			X	X
9. decticus		R	X	
10. diantaeus			X	X
11. dorsalis			X	X
12. excrucians			X	X
13. fitchii			X	
14. flavescens			X	X
15. hexodontus	Tundra		X	X
16. impiger	Tundra		X	X
17. implicatus			X	
18. intrudens			X	X
19. nigripes	Tundra		X	X
20. pionips			X	X (?)
21. pullatus	Alpine		X	X
22. punctodes		L	X	
23. punctor			X	X
24. rempeli	Tundra	L, R	X	
25. riparius			X	X
26. stimulans			X	
27. trichurus			X	
28. vexans			X	X
29. Culex territans			X	X
30. torrentium				X
31. Anopheles earlei			X	
32. maculipennis				X
33. Culiseta alaskaensis			X	X
34. annulata				X
35. bergrothi		L		X
36. impatiens			X	
37. incidens			X	
38. morsitans			X	X
			32	23

The relationships between these mosquitoes in North America and Eurasia are very close. At the present time 32 species are known from North America and 23 from Eurasia. The larger number from North America is due in large part to finer distinctions being made between species particularly in the *Aedes punctor* and *A. communis* groups. For example, while *A. hexodontus* has not been reported from Eurasia, a study of the range of variation of *A. punctor* in Norway showed the presence of typical *A. hexodontus*.

At present only half of the species, 19 out of 38, are known to occur in both continents. Many of the species reported from only one continent are represented in the other by a very similar or perhaps synonymous counterpart. *Anopheles maculipennis* of Eurasia is represented in northern North America by a species of this complex known presently as *Anopheles earlei*. Future study may show that certain of the presently recognized species of *Aedes* and *Culiseta* are the same or very closely related forms.

The greatest affinity between the northern continents is shown by the characteristic tundra mosquitoes. This group includes *Aedes nigripes* (Figs. 4 and 12), *A. impiger* (formerly *A. nearcticus*) (Figs. 5 and 13), and *A. hexodontus* (Fig. 6). *Aedes nigripes* extends throughout the tundra of North America and Eurasia and is characteristic and limited to this area. It is the most northern occurring mosquito in the world. *A. impiger* and *A. hexodontus* are characteristic of the arctic tundra but in addition occur in alpine habitats and extend southward near or above timberline in the mountains beyond the arctic zone. These three species constitute the true arctic mosquitoes, although other species extend into this area.

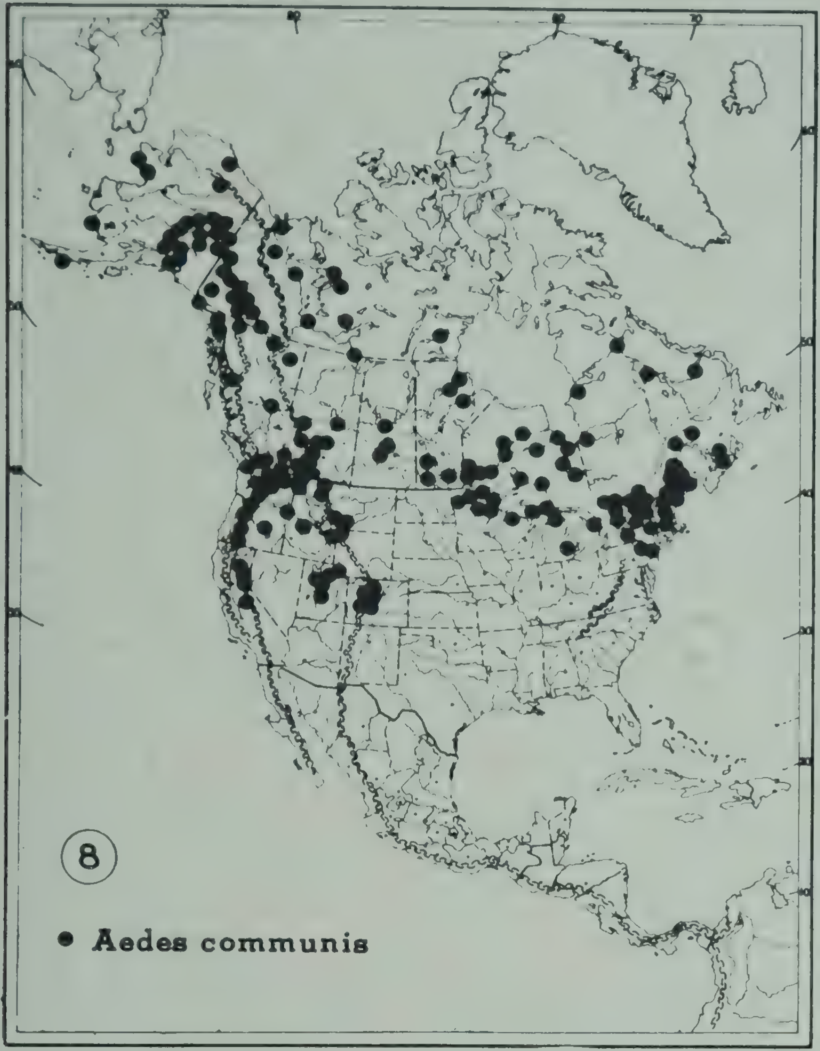
The typically alpine mosquitoes *A. pullatus* (Fig. 14) and *A. cataphylla* occur in mountains or rocky areas and while they occur in both tundra and muskeg areas they should be characterized as arctic-alpine and boreal-alpine. In North America these mosquitoes, together with arctic and certain subarctic species, occur at or near sea level in the northern

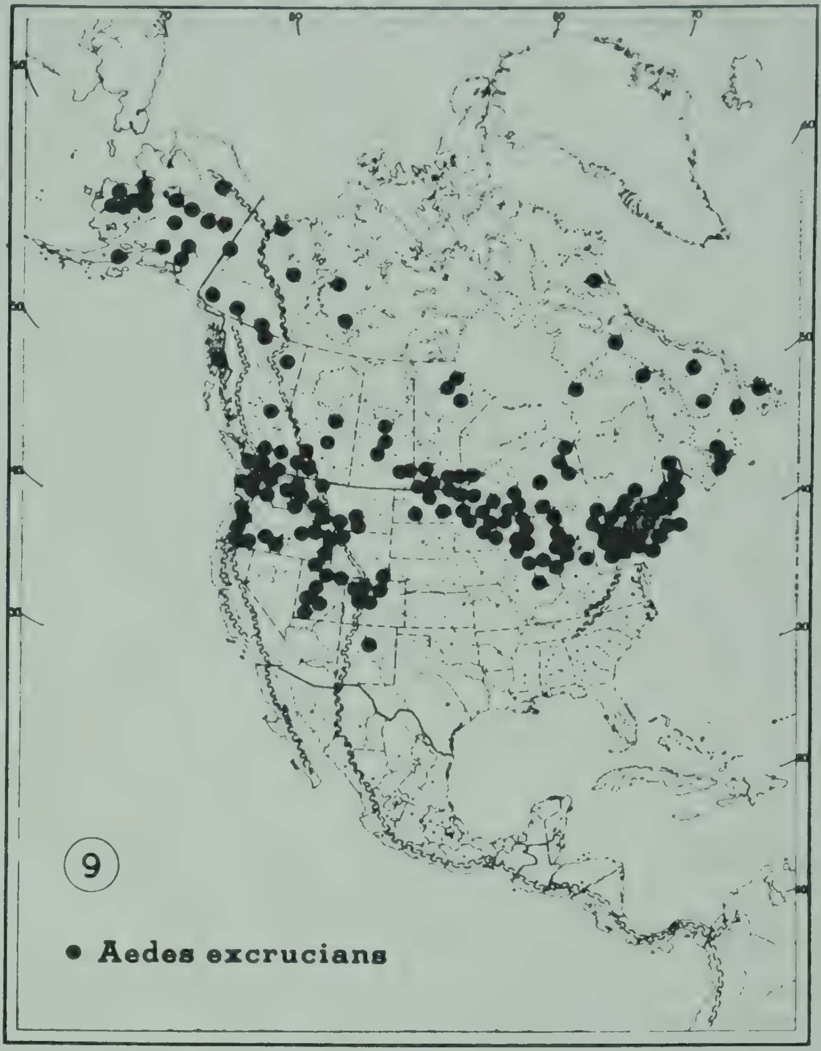


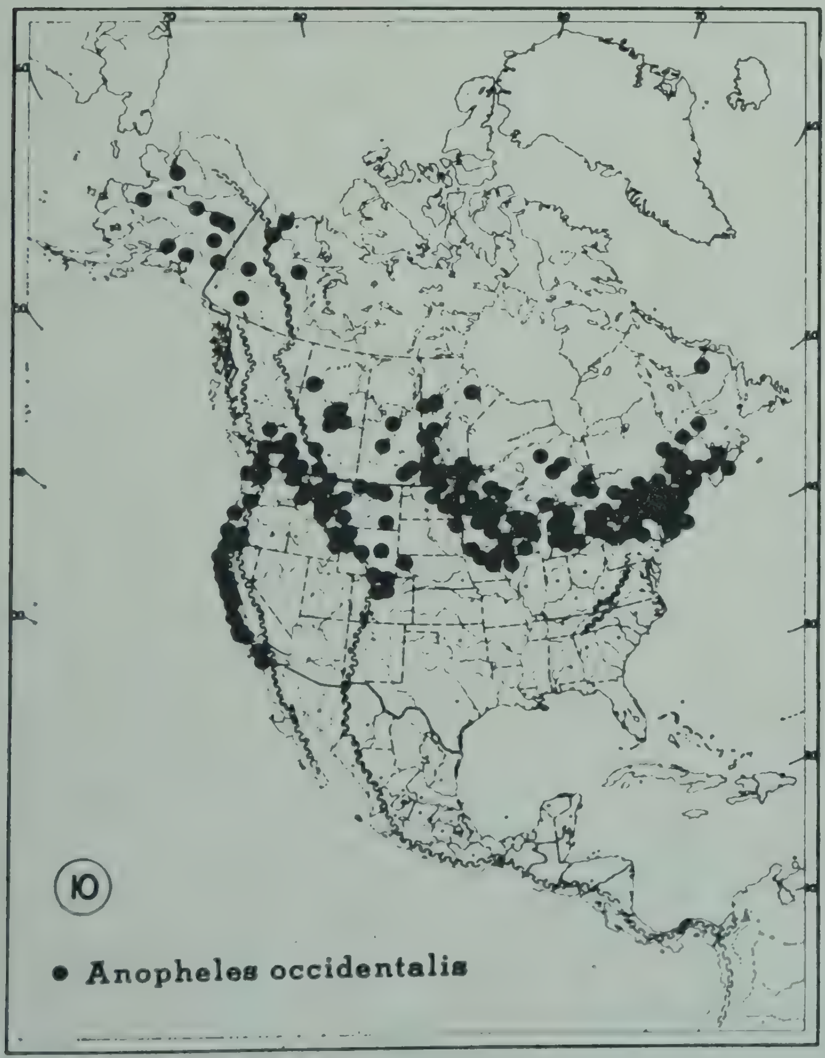
Figs. 4-7. North American distribution of *Aedes* spp. 4, *nigripes*. 5, *impiger* (formerly *nearcticus*). 6, *hexodontus*. 7, *punctor*.

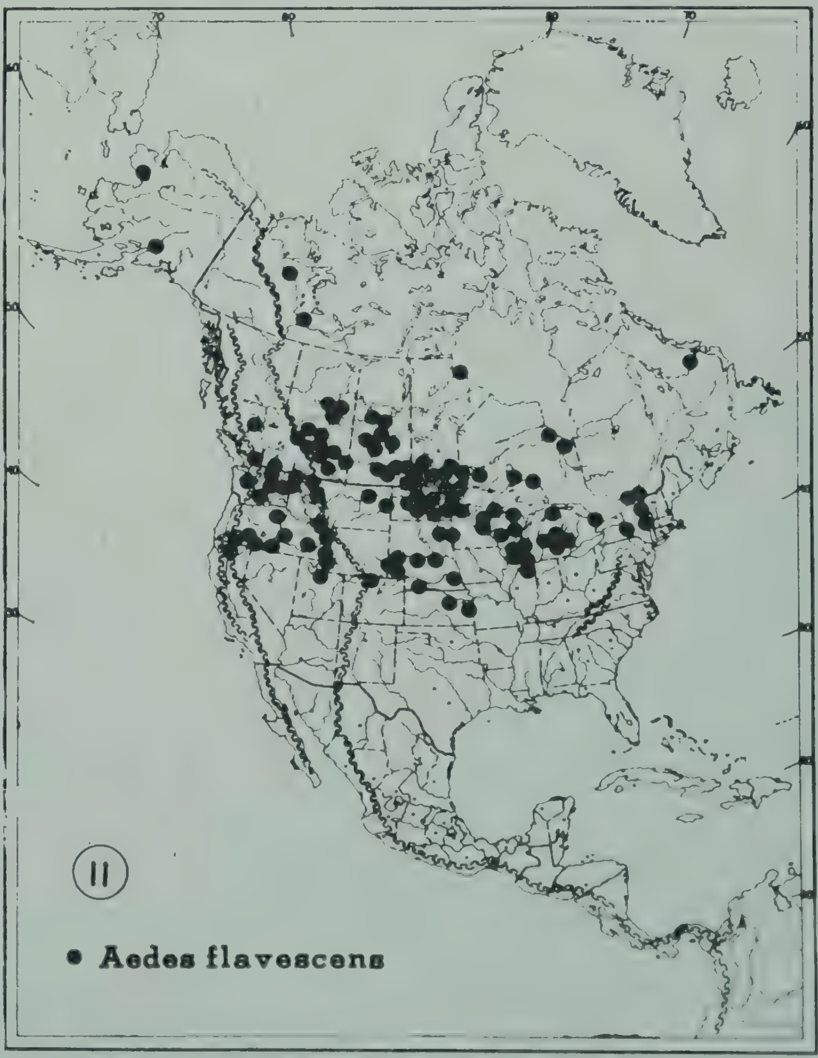
areas. Further south they are restricted to near timberline in the higher elevations, and in the Rocky Mountains occur up to 13,000 feet altitude or above (Fig. 3).

The subarctic transcontinental coniferous forests are inhabited by many typical taiga or muskeg species of which *Aedes punctor* (Figs. 7 and 15) and *A. communis* (Figs. 8 and 16) are most characteristic and abundant. Other species typical of this area include *Aedes cantans*, *A. decticus*, *A. diantaeus*, *A. excrucians* (Figs. 9 and 17), *A. fitchii*, *A. implicatus*, *A. intrudens*, *A. pionips*, *A. trichurus*, *Anopheles earlei* (Formerly part of *occidentalis*) (Fig. 10), *Culiseta alaskaensis* (Fig. 18), *C. bergrothi*, *C. impatiens*, *C. incidens*, *C. morsitans*.









Figs. 8, 9, 11. North American distribution of *Aedes* spp. 8, *communis*. 9, *excrucians*. 11, *flavescens*.

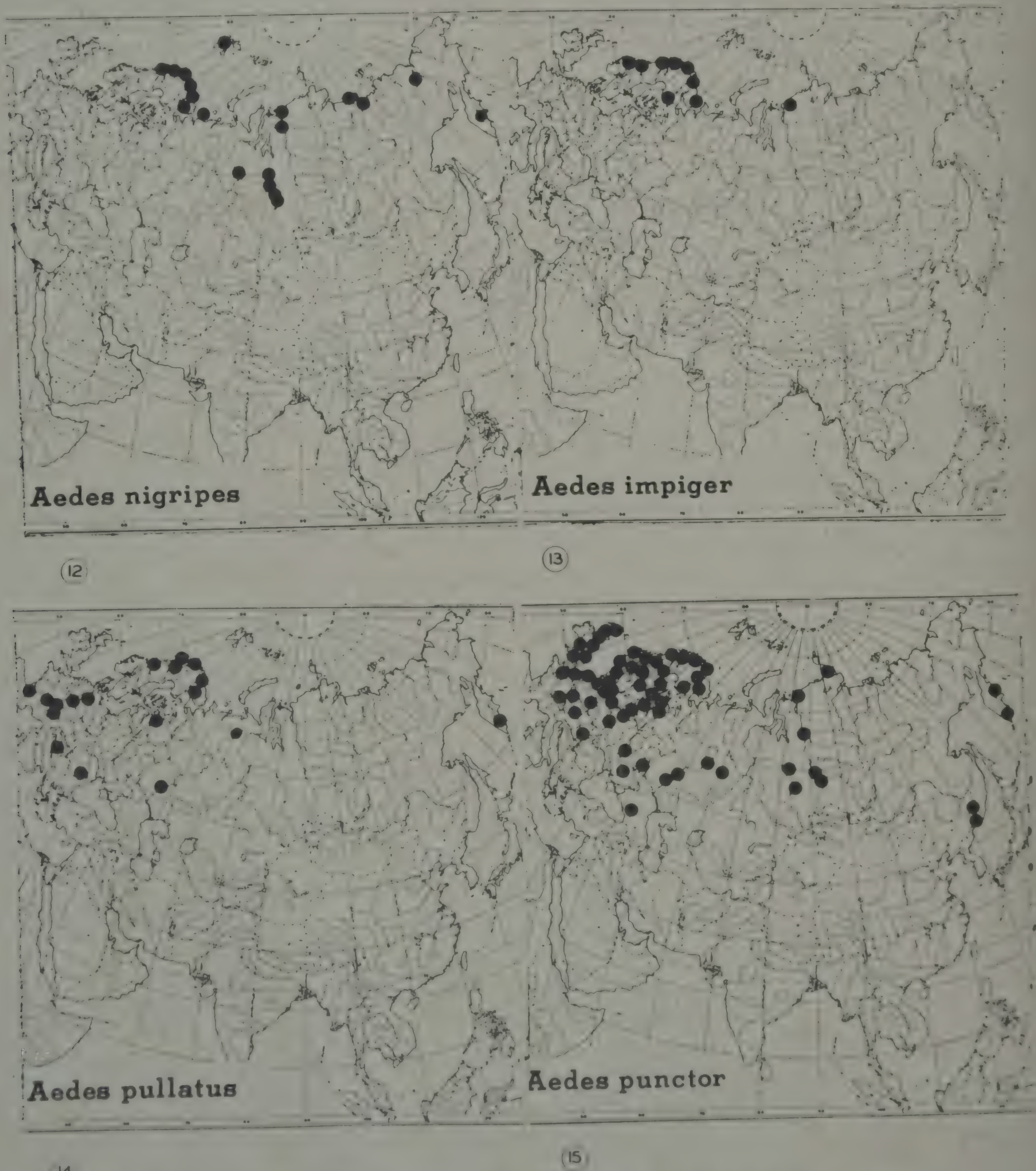
Fig. 10. North American distribution of *Anopheles earlei* (formerly part of *occidentalis*, now also known from California, Oregon, and Washington).

These species occur in enormous numbers in the taiga and most extend southward in the mountains or in heath bogs in the deciduous forest.

Species typical of the great plains and the aspen parklands to the north, but which extend into the northern areas include certain species which frequently occur in saline water such as *Aedes campestris*, *A. caspius*, *A. dorsalis*, *A. flavescens* (Fig. 11), and *A. riparius*. These species are in general wide-ranging and have scattered distribution in the far north.

Several northward extending species are more cosmopolitan and are widely dispersed in a number of ecological communities. They are most abundant in river valleys particularly in the northern areas. These species include *A. canadensis*, *A. cinereus*, *A. sticticus*, *A. vexans*, *Culex territans*, and *C. torrentium*.

The species discussed so far are wide-ranging and well distributed. There are, however, several species which are more restricted to specific ecological communities. These include *A. punctodes* limited to the salt marsh and river valleys in Alaska, *A. aboriginis* occurring

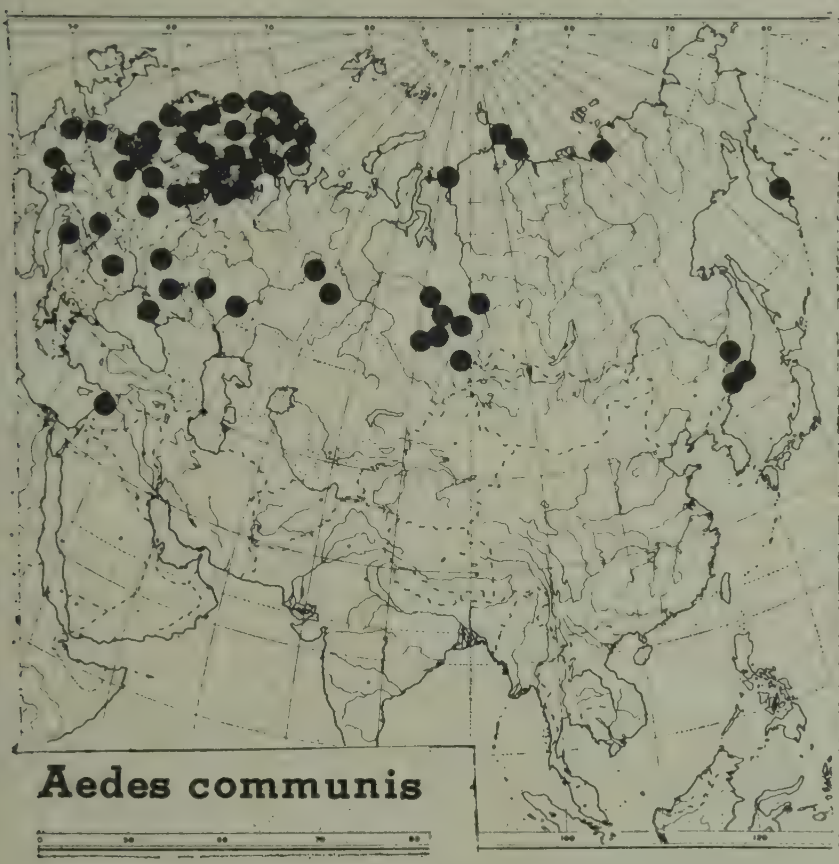


Figs. 12-15. Eurasian distribution of *Aedes* spp. 12, *nigripes*. 13, *impiger*. 14, *pullatus*. 15, *punctor*.

in the Pacific coastal conifer forest, and *A. abserratus* (formerly *A. implacabilis*) limited to the white Pine-Hemlock forest of the St. Lawrence River and Great Lakes area.

Rarer species whose distributions are not so well known include the recently described *A. rempeli* of North America and *A. beklemisheva*, and *A. grandilarva* of Asia.

Except for the rarer or newly described mosquitoes, these species usually have continuous distributions, with one outstanding exception, *Aedes pullatus*. This species is abundant in the western mountains of North America, absent in interior Canada, and present in Ungava, Baffinland, and Newfoundland. In Eurasia this species is found in northern Scandinavia, the Alps and higher European mountains, Yugoslavia, the Transylvanian Alps, Saratow, and is then unknown until nearly 5,000 miles eastward to Kamchatka. Natvig (1948) considers *A. pullatus* to be a survivor of the Würm glaciation in Norway. In the western Hudson Bay region this species is absent from very suitable habitats and this might be explained by the relatively recent glaciation in that area. Its presence in eastern Hudson Bay may be due to survival during the Pleistocene glaciations in Eastern North America.



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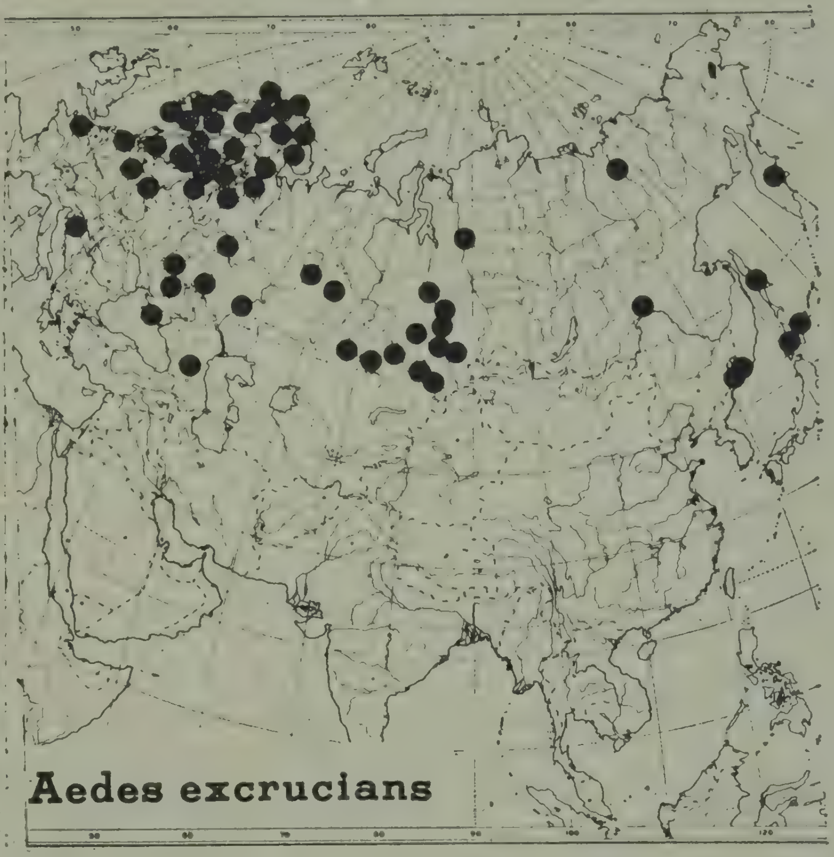

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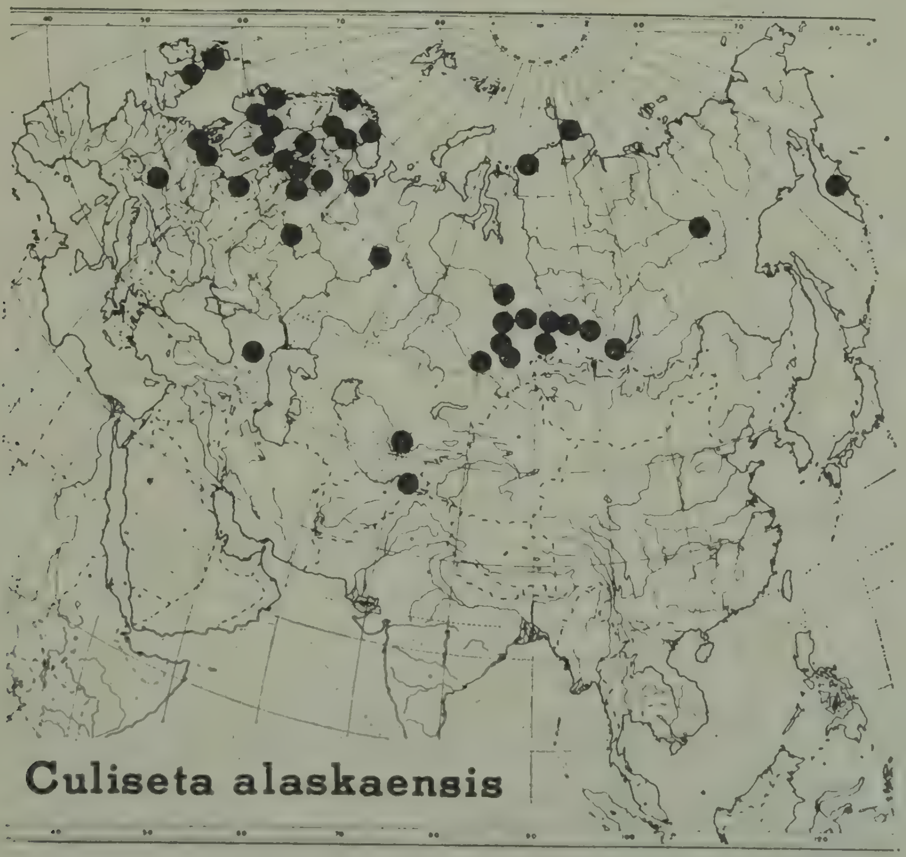

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Figs. 16, 17. Eurasian distribution of *Aedes* spp. 16, *communis*. 17, *excrucians*.

Fig. 18. Eurasian distribution of *Culiseta alaskaensis*.

REASON FOR ABUNDANCE

The extensive arctic and subarctic regions offer an almost unlimited area of growth and expansion for any type of organism which is able to survive the long and extremely cold winters. Any organisms able to withstand this environmental extreme become eligible for exploitation of an enormous area with very little competition. The mosquitoes of the arctic and subarctic regions have been able to overcome this environmental barrier by overwintering in the inactive egg stage. The eggs are usually laid in depressions and are somewhat protected from the excessive cold and dryness. In the subarctic certain species are able to survive by hibernating in the adult stage in protected places.

The arctic tundra and northern conifer forest offer a unique opportunity for the production of enormous numbers of mosquitoes due to the great abundance of standing water. This is formed by melting of the snow, ice, and permafrost during the short spring and early summer. The amount of surface standing water is very great because of the relatively small amount of gradient and relief over extensive areas, the very poor drainage caused by the permafrost or temporary soil ice, and the large amount of snow and ice melt water supplemented by spring rains in some areas. This standing water contains much dissolved and suspended nutrient material due to the very slow decomposition of organic material in the north. Sufficient growth of plankton and microorganisms occurs during the short but intense growing season to furnish an adequate food supply. In this region there are relatively few competitors, predators, or parasites in mosquito habitats. The mosquitoes are admirably adapted to these conditions, since their short larval growing period is synchronized with the first warming of the area. The remainder of the warm season then permits sufficient time for the adults to mate, obtain blood or other meals, and to lay eggs.

Control is very diffcult because the species disperse and migrate widely. Even though the mosquitoes are eliminated by insecticide spraying for many square miles around a site, the mosquitoes migrate back into the area in a few days. At Churchill, the author released about 3 million radiophosphorus labeled *Aedes communis* adults and observed dispersal up to one mile in spruce forest. Other species migrate much further and *A. flavescens* was found by other workers to migrate 6 miles. *A. hexodontus* males were observed by the author to migrate several miles along a railroad bed.

The advance of civilization into the arctic and subarctic frequently causes an increase of mosquitoes in the populated areas, due to increasing the breeding areas in wheel tracks and ditches, and in providing more blood meals for the mosquitoes. Control appears to be dependent on exploiting any weaknesses in the biology of the species. Use of mosquito predators and parasites occurring in the northern areas should be considered in future control programs.

REFERENCES

Natvig, L. R. 1948. Contributions to the knowledge of the Danish and Fennoscandian Mosquitoes. Culicini. *Norsk. Entom. Tidsskrift. Suppl* 1: 567 pp. Oslo.

Stackelberg, A. A. 1937. Faune de l'URSS, Insectes Dipteres, Family Culicidae (Subfamily, Culicinae) 3(4): 258 pp. [In Russian] Moscow-Leningrad.

Classification and Distribution of Arctic and Subarctic Simuliidae[1]

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INTRODUCTION

Knowledge of the immature stages and, in general, of the ecology of the Simuliidae of northern Canada and Alaska has so greatly increased in recent years that it is now possible to draw firmer conclusions than heretofore about the relationships of the species and to express these relationships more fully in our classification. Of roughly fifty northern species only one or two are still unknown in both larval and pupal stages and in a few more, the larva still remains to be discovered. A great deal of the credit for this increased knowledge must go to the United States Bureau of Entomology whose Alaska Insect Project carried out intensively in 1947 and 1948, has resulted in very important publications on the immature stages and ecology of the family. The Canadian Northern Insect Survey has, in the meantime, covered much arctic and subarctic territory, resulting in the accumulation of valuable material and information, the study of which, has, in large part, formed the basis for the present paper.

CLASSIFICATION

The Simuliidae may be divided into two subfamilies, Prosimuliinae and Simuliinae, mainly on the basis of the type of cocoon constructed by the larva. I do not believe, as Rubtzov (1940, page 108) apparently does, that the type of cocoon is dependent on the conditions of the chosen habitat and not, therefore, of much phyletic importance. On the contrary, the evidence seems to me to point the other way. In observing colonies of black flies in streams, it is striking that under exactly similar conditions the most diverse types of cocoons will be found side by side. From a mass of neat slipper-shaped cocoons of *Simulium venustum* Say on a submerged branch will protrude at intervals the tall, elaborately woven basket-like structures of *Simulium corbis* Twinn while in the notches of the twigs may be the untidy sleeves of *Cnephia dacotensis* (D. & S.). In the crevices on the undersurface of small stones in shallow ditches will be found the almost naked pupae of *Cnephia mutata* (Mall.) as well as the broad flat 'slipper' cocoons of *Simulium latipes* Mg. Many other such examples could be given so that it cannot be doubted that the larva spins its cocoon as a result of strong hereditary instinct upon which the special attributes of the local environment have little influence. Confirmation of this is perhaps to be found in the structure of the ventral surface of the larval head capsule. It may be supposed that the more elaborate the design of the cocoon, the more flexibility is required in the neck region of the larva and it is noticeable that those species that make a mere gesture towards cocoon spinning have the ventral surface of the head capsule entirely sclerotized, whereas those species that spin elaborate cocoons have a large area of membrane, in the form of a cleft or invagination, in the posteroventral region of the head (Fig. 1).

Both the form of the larval head and the structure of the cocoon have an important bearing on the question of the origin of the whole family. It is already generally conceded that Simuliidae are most closely related to Tendipedidae but this relationship has been much more forcefully emphasized recently by the discovery of the new genera *Gymnopais* Stone and *Twinnia* Stone in which the larval mouth fans are absent, bringing the whole structure of the head capsule much nearer to the typical tendipedid type than was demonstrable before (Fig. 1). Furthermore, several types of cocoons constructed by species of *Prosimulium* are also found commonly in the Tendipedidae, especially the simple loosely-woven sac-like structure, the cocoon in which small silt particles are utilized and a third type, recently observed in western Canada in which the covering is a transparent gelatinous sheath.

Although black flies are usually thought of as inhabiting fast turbulent mountain streams, very many species in fact prefer only moderate current speeds, some of the most generalized forms, including several *Prosimulium* species, being found in ditches where the

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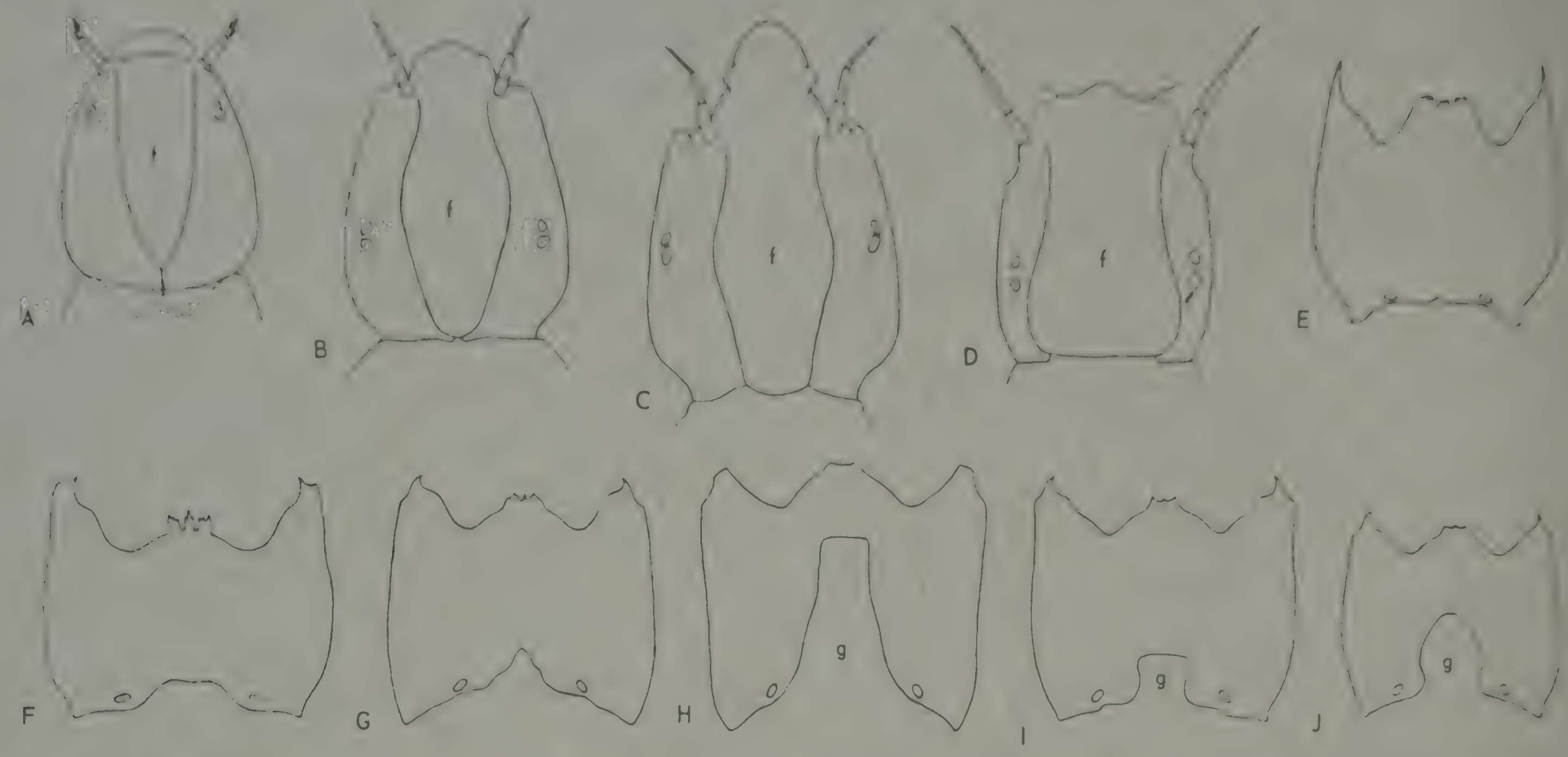

Fig. 1. A-D. Comparison of larvae of Tendipedidae and Simuliidae. Dorsal view of head of A. *Cardiocladius* Kieff., an orthocladiine midge living in rapid water, B. *Twinnia* St., C. *Gymnopais* St., D. *Simulium* Latr., showing progressive enlargement of posterior part of fronto-clypeal plate (f). E-J. Comparison of larvae of Simuliidae showing development of gular cleft (g) perhaps correlated with cocoon-spinning. Ventral view of head-capsule of E. *Gymnopais* St. (no cocoon), F. *Prosimulium* Roub. (cocoon, if present, shapeless), G. *Cnephia* subgen. *Mallochianella* V. & D. (no cocoon), H. *Cnephia* subgen. *Astega* End. (cocoon boot- or slipper-shaped), I. *Simulium* subgen. *Eusimulium* Roub. (cocoon slipper-shaped often with distinctive anterior process), J. *Simulium* s.str. (cocoon slipper-shaped).

current can only be detected in the shallowest stretches. It can thus be conjectured that both Tendipedidae and Simuliidae that now inhabit rapids and cataracts have evolved from forms living in static water.

In Prosimuliinae should be placed four genera namely *Gymnopais* Stone, *Twinnia* Stone, *Prosimulium* Roubaud and *Cnephia* Enderlein. There is no doubt that *Gymnopais* deserves generic status on characters of all stages. [The larvae lack mouth fans, the adult lacks pale thoracic hairs etc., and the pupal respiratory filaments are distinctive.] *Twinnia* is not so well founded. The larva is distinctive, without mouth fans, but the pupa and adult are hardly different from *Prosimulium*, in fact pupal filaments occur in *Prosimulium* spp. that closely resemble those of *Twinnia* spp. *Twinnia* should therefore perhaps be placed as a subgenus of *Prosimulium*. It is convenient to recognize *Helodon* Enderlein as a subgenus distinct from *Prosimulium* s.str. for those species having a well-developed tooth at the base of the claw. There seem to be very few cases in which species with simple and strongly-toothed claws are closely related to one another. The toothed claw, when it occurs, seems to have group significance and is evidently related to the biting habit. Within *Helodon*, however, a western and an eastern group of species should be recognized, the western group more closely related to the subgenotype *ferrugineum* Wahlberg in being composed of somewhat slender species with elongate legs and unusually large wings. Both groups are distinct from *Prosimulium* s. str. in lacking a long pointed ovipositor.

In *Cnephia*, as already mentioned, four subgenera may be recognized: *Cnephia* s.str., *Mallochianella* Vargas and Diaz, *Astega* Enderlein and *Ectemnia* Enderlein, the first two more distinctively prosimuliine than the last and all four readily separated from one another on characters of all stages.

In the Simulinae there is a single large genus, *Simulium* Latr. It would perhaps be useful to retain *Eusimulium* Roubaud as a full genus, but the adult characters are apparently not constant enough to warrant it, and it is here treated as a subgenus of *Simulium*. Other subgenera that seem to be useful concepts are: *Schönbaueria* Enderlein (type *Schönbaueria matthiesseni* End.) for a single North American species *furculata* (Shew.) (*Eusimulium furculatum* Shew. 1952) which is apparently close to the European *Schönbaueria pusilla* (Fries); *Byssodon* Enderlein (type *Simulium forbesi* Mall. equals *Simulium meridionale* Riley), for those species that, despite the bidentate female claw, are obviously different from *Eusimulium*; *Gnus* Rubtzov (type *Simulium decimatum* D.R. & V.) for a very homogeneous holarctic group that includes our worst cattle scourge *Simulium arcticum* Mall.

The adults have the base of the female claw minutely toothed and the larvae spin cocoons with elaborate cross-woven loops surrounding the opening; *Aspathia* Enderlein (type *Simulium hunteri* Mall.) for this western species and the eastern *Simulium parnassum* Mall: *Neosimulium* Rubtzov. (type *S. vittatum* Zett.) for this most distinctive species and its close relative *S. argus* Will.; finally in *Simulium* s.str., which seems to be at present not well-defined, are placed our common holarctic species *Simulium venustum* Say and other species that appear to be more or less closely related to it.

DISTRIBUTION

Prosimulium AND OTHER PRIMITIVE GENERA

In the northwestern corner of the continent a heavier concentration of species of the holarctic genus *Prosimulium* Roub. (Fig. 2A) occurs than is to be found elsewhere in its range. Of fifteen species reported from North America, ten are found here, five of them being endemic. In addition, three species belonging to the even more primitive genera *Gymnopais* St. and *Twinnia* St. also occur. The main distribution of these northwestern species is Cordilleran, five of the species extending a varying distance south in the Rocky Mountains and coastal ranges with three being reported from California. One species is Beringian, occurring as far east as Lake Baikal. Two species are arctic, one of them being circumpolar. There are also two North American subarctic species and one widespread circumboreal species.

On the eastern side of the continent another concentration of *Prosimulium* occurs, consisting of five species additional to the transcontinental forms already mentioned and there is also another species of *Twinnia*. Although apparently mostly confined to the Appalachian Mountains in the South, the northern range of these eastern species includes in some cases all the eastern part of the Boreal Forest as far as the Manitoba-Ontario border. This distribution has been called here Laurentian. There appears to be a gradual falling-off in numbers of species both north and south of the upper St. Lawrence valley, several species being recorded in New York State that have not been found in adjacent Canadian territory and vice versa.

Our present knowledge of the general distribution of *Prosimulium*, *Gymnopais* and *Twinnia* in Canada indicates that they are absent from a broad strip west of Hudson Bay from the southern prairie to the Arctic Ocean and including the islands west of the Boothia Peninsula. It does not seem probable, from the surveys that have already been made, that these genera will now be found to exist continuously across the continent in the parkland of central Saskatchewan, but it is possible that the two arctic species *Prosimulium ursinum* Edw. and *Gymnopais holopticus* St. will be found on the tundra between Boothia and the Mackenzie Delta where they are now unknown although they have been found on Southampton and Baffin Islands and in many localities in Alaska.

GENUS *Cnephia* ENDERLEIN

As has already been remarked, this genus, as presently constituted, is evidently polyphyletic [including some forms which are allied to *Prosimulium* and some more closely related to *Simulium*]. Of the two subgenera with more generalized characters *Cnephia* s.str. is North American (Fig. 2B) while *Mallochianella* Vargas and Diaz is holarctic (Fig. 2C). Each have both arctic and Hudsonian elements in Canada and Alaska and the same or closely-related elements extend southward from the Hudsonian to the Upper or Lower Austral Zone. The two arctic species, *Cnephia* (*Cnephia*) *eremites* Shew. and *Cnephia* (*Mallochianella*) *emergens* St., unlike *Prosimulium*, are found continuously across the tundra from Baffin and Southampton Islands to Alaska. It is possible that the last-named species is circumpolar. The two subarctic species *Cnephia* (*Cnephia dacotensis* (D. & S.) and *C.* (*Mallochianella*) *mutata* (Mall.) occur from the Upper Austral in S. Dakota, Iowa and the Atlantic seaboard north to the edge of the tundra at Churchill and Goose Bay. *C. mutata* also occurs widely in the western mountains from the Alaskan panhandle to California and has recently been reported from Japan. The two other subgenera of *Cnephia*, namely *Astega* End. and *Ectemnia* End., are sufficiently distinct both from each other and from the rest of the genus that they are best discussed separately. *Astega* is circumpolar and predominantly arctic and alpine (Fig. 2D). Its strong affinity with *Simulium* is shown in the well-constructed boot-shaped cocoon and lack of terminal hooks on the pupa and the

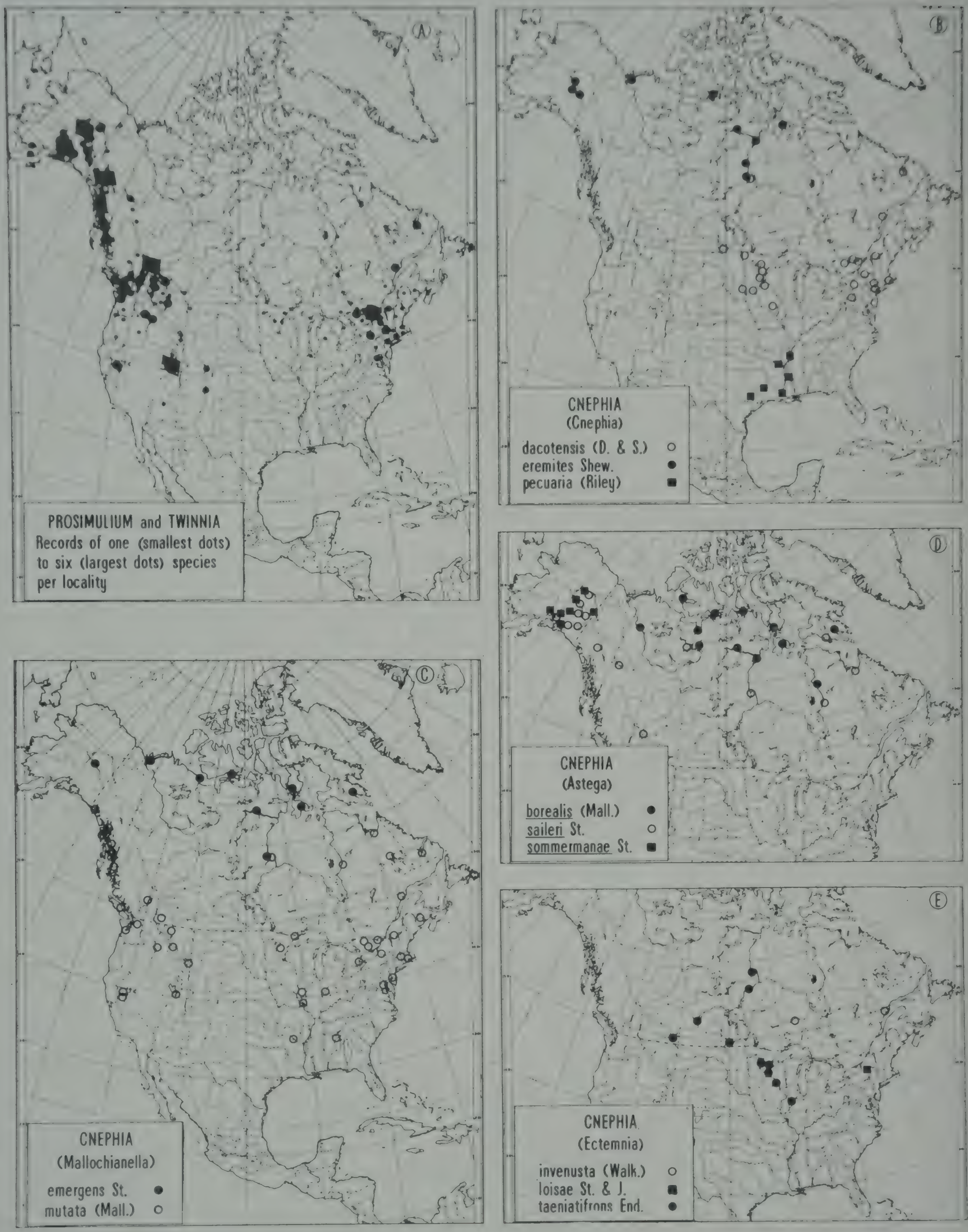
Ⓐ
PROSIMULIUM and TWINNIA
Records of one (smallest dots) to six (largest dots) species per locality
Ⓑ
CNEPHIA
(Cnephia)
dacotensis (D. & S.) ○
eremites Shew. ●
pecuaria (Riley) ■
Ⓒ
CNEPHIA
(Mallochianella)
emergens St. ●
mutata (Mall.) ○
Ⓓ
CNEPHIA
(Astega)
borealis (Mall.) ●
saileri St. ○
sommermanae St. ■
Ⓔ
CNEPHIA
(Ectemnia)
invenusta (Walk.) ○
loisae St. & J. ■
taeniatifrons End. ●

Fig. 2. A. Distribution and relative abundance of *Prosimulium* and *Twinnia* in North America. The smallest dots represent records of one species, the next size two species, the next three or four species, and the largest five or six species. B-E. Distribution of *Cnephia* End.

supplementary hair tuft on the mesopleural membrane is also a simuliine character but the long somewhat matted thoracic and abdominal hair of the males, somewhat elongate basal section of the radius and lack of calcipala and pedisulcus are equally suggestive of prosimuliine relationship. The group must have survived in Beringia and possibly also in the southern Cordillera. *Ectemnia* End. (which incidentally includes the long-unrecognized species *Simulium invenustum* Walker from St. Martin's Falls) shows strong affinity with *Eusimulium* in the large basal tooth of the female claw and in the presence of posterior ventral papillae in the larvae. However, the pupa has small apical hooklets and the attachment of the cocoon to a thick half-inch-long silk rope woven by the larva, is a habit not known in any other group. The adult characters show stronger affinity with Prosimuliinae. The present known distribution of the group (Fig. 2E) makes it probable that it is derived from forms inhabiting the central Mississippi basin. Only one of the three known species extends north of the Canadian zone. This is *taeniatifrons* End. which is found on the upper Mississippi from Illinois to Minnesota, on the South Saskatchewan and other big rivers of the Canadian prairies as far west as the Alberta-Saskatchewan border and on the Nelson and Churchill Rivers in northern Manitoba. *Invenustum* Walk. is known only from two widely separated localities in central Ontario and Quebec. *Loisae* S. & J. is reported only from northern New York State. The habitat preferences of the subgenera of *Cnephia* are as diverse as their morphological differences and distribution patterns would suggest. *Cnephia* s.str. species are lake-outlet species, *Mallochianella* species prefer shallow ditches and rivulets with moderate current speeds. *Ectemnia* species inhabit large- and medium-sized rivers at depths of several feet in fast unbroken water. *Astega* species live in small turbulent moderately shallow streams with rocky beds. Speculation as to the relation of these groups to each other and to other genera seems profitless at present. Several undescribed Canadian species remain to be studied and these may prove to have characters intermediate between some of the above groups. I place *Cnephia* with Prosimuliinae at present chiefly on the length of the basal section of the radius and the lack of opalescent markings on any of the forms. The pupae of *Cnephia* s.str. and *Mallochianella* and the larva of the latter are very like *Prosimulium*.

GENUS *Simulium* LATREILLE

SUBGENUS *Schönbaueria* ENDERLEIN

A single species *Schönbaueria furculata* (Shew.) occurs in North America (Fig. 3A). It is mainly confined to the Shield. It is not found in the arctic islands and is rare west of the Mackenzie but develops enormous populations in the sparsely-treed interior of northern Quebec and on the tundra on both sides of Hudson Bay. Its dispersal appears to have been from the east. Recently both *Eusimulium baffinense* Tw. and *S. furculata* have been found in localities far south of their normal range, the first in Utah, the second in eastern Ontario about 150 miles west of Ottawa.

SUBGENUS *Eusimulium* ROUBAUD

In this large subgenus, besides several widespread subarctic or boreal species occurring in both hemispheres, there is in North America an interesting arctic and Hudsonian species, *Eusimulium baffinense* Twinn, occurring commonly in Alaska and on the tundra west of Hudson Bay, less commonly in Ungava and the adjacent arctic islands (Fig. 3A). It appears to be derived from Beringia and there is a closely related species occurring in Swedish Lapland that may be undescribed. There is one Beringian species of *Eusimulium*, namely *bicornis* D.R. & V., reported on this continent only from Alaska but occurring across the northern palaearctic region to Scandinavia. All other North American species are subarctic rather than arctic in distribution. The widespread holarctic species have already been mentioned. They are *aureum* Fries, *latipes* Mg. and *costatum* Fries (= *pugetense* D. & S.?). Because of lack of data I hesitate to mention any others except the group that includes *canonicolum* D. & S. and *euryadminiculum* Davies. The former species has been taken once at Baker Lake, N.W.T. The type locality is the Yellowstone Canyon in Wyoming and it is known also from the parkland of central Saskatchewan and from localities in Idaho, Colorado, Utah and California. *Euryadminiculum* Davies is at present known only from eastern Ontario, the east coast of Hudson Bay and Labrador. *Johannseni* Hart is a transition and Upper Austral species occurring from Idaho to Massachusetts. In central Saskatchewan there appear to be two further species weakly defined on pupal characters. Unlike most *Eusimulium*, the members of this group develop in large torrential streams. *Euryadminiculum* Dav. is on the wing in mid-May in eastern Canada, and *johannseni* Hart appears at about the same time in Illinois. [Later collection dates for *canonicolum* in southwestern U.S. suggest that a second generation may appear there.] The general distribution pattern of the group suggests that the Canadian species have spread from the upper Mississippi and Missouri basins rather than from the mountain systems. The species are somewhat larger than is usual in *Eusimulium* and are superficially very similar to each other. There is evidently still much to be learned about their distribution and errors of identification probably give, at present, an inaccurate picture. An especially wide distribution is noticeable among species of *Eusimulium* and it seems possible that dispersal has been assisted by birds on

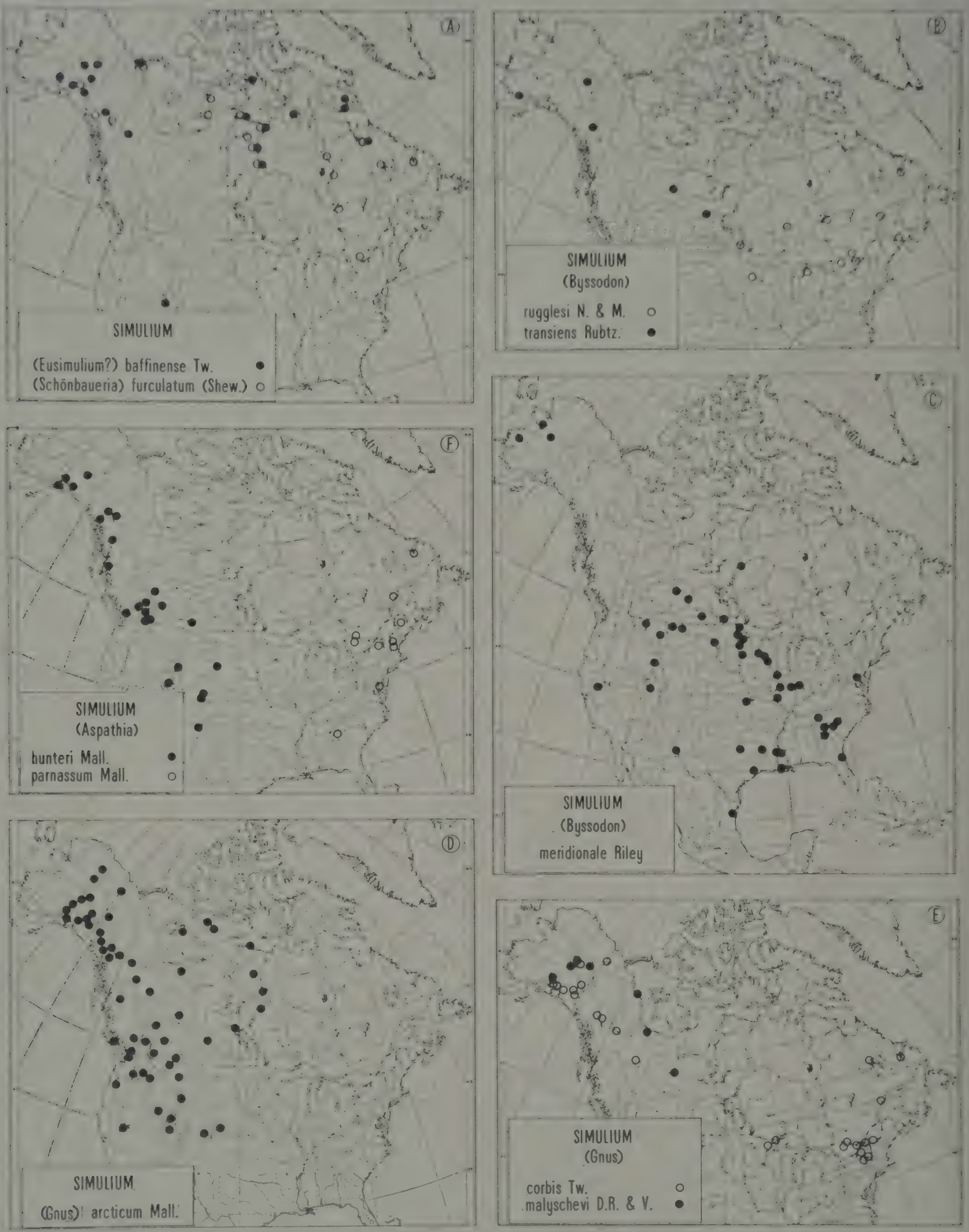
(A)
SIMULIUM
(Eusimulium?) baffinense Tw. ●
(Schönbaueria) furculatum (Shew.) ○
(B)
SIMULIUM
(Byssodon)
rugglesi N. & M. ○
transiens Rubtz. ●
(F)
SIMULIUM
(Aspathia)
hunteri Mall. ●
parnassum Mall. ○
(C)
SIMULIUM
(Byssodon)
meridionale Riley
(D)
SIMULIUM
(Gnus) arcticum Mall.
(E)
SIMULIUM
(Gnus)
corbis Tw. ○
malyschevi D.R. & V. ●

Fig. 3. Distribution of *Simulium* s.l., A. *Eusimulium* (?) *baffinense* Tw. and *Schönbaueria furculatum* (Shew.), B. and C. *Byssodon* End., D. and E. *Gnus* Rubtz., F. *Aspathia* End.

which many of the species undoubtedly feed. Observations are few but in *Simulium rugglesi* N. & M., a species with similar claw structure to *Eusimulium*, it has been noted that engorged flies remain beneath the feathers for some time and thus, theoretically, could be carried great distances.

Subgenus *Byssodon* Enderlein

This is a small group of four species that feed on birds and have claws similar to those found in *Eusimulium* but in other respects are closer to *Simulium* s.str. [They differ from *Eusimulium* in having the basal section of the radius bare, the legs with pale markings and the ground colour of the thorax not completely obscured by decumbent pile]. The subgenotype, *S. meridionale* Riley, is somewhat removed from the other species in being entirely dark-legged. It is a southern species, occurring across the continent from Florida to California but is especially common in the Mississippi-Ohio-Missouri Basin from Louisiana to the Canadian border (Fig. 3C). In Canada it has become well-established in the Red-Souris-Saskatchewan system and has been taken as far north as Gillam on the Nelson River 100 miles from Hudson Bay. It has for some reason failed to become established in the St. Lawrence system. It apparently occurs on the lower Yukon River in western Alaska but has not been recorded west of the continental divide from Oregon to Yukon Territory. It seems to be clearly a 'big river' species. Of the three other species which appear to be closely related to one another, *transiens* Rubtzov is Beringian. Described from eastern Siberia it occurs in Alaska, Yukon and central Saskatchewan (Fig. 3B). *Rugglesi* N. & M. is an eastern Hudsonian and Canadian species having a typical "Laurentian" distribution (Fig. 3B). *Slossonae* D. & S. is apparently Austroriparian, being found in sluggish streams from Florida to Virginia.

SUBGENUS *Simulium* SENSU STRICTO

Imperfect knowledge of many of the Palaearctic forms makes it difficult to decide how to restrict the subgenus *Simulium*. Included in it for the present are the two common circumboreal species, *venustum* Say and *tuberosum* Lundstrom, and also the widespread species, *decorum* Walker, which is considered to be North American only and not circumboreal as some authors claim. The fact that the female of *decorum* has an exceptionally hump-backed thorax, approaching the normal male condition, has been overlooked by all workers since Hearle (1932) first drew attention to it.[3] I have verified it in Walker's types and it is apparently uniform in North American specimens, except those taken on the tundra from Hudson Bay to the Mackenzie Delta. It is evidently not a feature of the European *nölleri* Friederichs, *subornatum* Edwards, etc. *Decorum* is a lake-outlet species occurring across the continent in the Hudsonian and Canadian zones. The tundra population must be considered at least subspecifically distinct. In this subgenus are also placed *Simulium luggeri* Nicholson & Mickel, a big-river species closely related to *jenningsi* Malloch, an austral and southeastern Canadian form. It has apparently spread into Canada in postglacial times by way of the upper Mississippi and Red Rivers and is now found in the Red-Souris (and presumably Saskatchewan) system, in the Churchill River at Hudson Bay and in the Mackenzie and its tributaries as far north as Norman Wells.

SUBGENUS *Gnus* RUBTZOV

The subgenus *Gnus* Rubtzov comprises a readily-recognized holarctic group breeding mainly in torrential rivers and streams of large or medium size. There are three described species in the north. *S. malyschevi* Rubtz., with a Beringian distribution, occurs here only in Alaska and the Mackenzie river system as far south as McMurray on the Athabasca River (Fig. 3E). *S. arcticum* Malloch, with a widespread western arctic, subarctic and Cordilleran range, from Alaska to Hudson Bay and in the south from California to eastern Colorado (Fig. 3D), breeds in the Saskatchewan river system in outbreak numbers causing important losses among livestock, especially cattle. It is surprising that such a widespread species should have so far been unreported in Siberia. The third species, *S. corbis* Twinn, is probably holarctic. It has a discontinuous distribution in North America, being present in the Hudsonian and Canadian zones on both sides of the continent but unknown from Hudson Bay to the Rockies (Fig. 3E). The reason for this discontinuity is not clear since the species does not now occupy, except in Alaska, any territory that escaped glaciation. The species of this group are distinguished by the construction of the cocoon which is boot-shaped with an elaborately woven rim of net- or basket-work surmounting the opening.

SUBGENUS *Aspathia* ENDERLEIN

The type of this subgenus, *S. hunteri* Mall., has, in the female, an unusually long claw bearing a small tooth some distance from the base. *Simulium parnassum* Mall. is the only other described North American species having the same type of claw and the two species are, therefore, provisionally placed together although, on other grounds, their close relationship may be questioned. The larvae of both species construct a slipper cocoon and on this account *hunteri*, which might otherwise be grouped with *articum* and its relatives, can safely be separated from them. However, the pupal filaments differ greatly being multi-branched in *hunteri* and six-branched in *parnassum*. *S. hunteri* is a Cordilleran species ranging from Alaska to New Mexico (Fig. 3F). It has also been found in the Cypress Hills of southwestern Saskatchewan and on the western border of South Dakota. *S. parnassum* is eastern, occurring from the Hudsonian in Labrador to the Upper Austral of Virginia (Fig. 3F). In Canada the adults of *parnassum* do not appear till midsummer.

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[3] See also Stone and Jamnback (1955) p. 64.

SUBGENUS *Neosimulium* RUBSTZOV

The single northern species of this subgenus, *Simulium vittatum* Zett., is extremely widespread and abundant in continental North America from the Hudsonian to the Upper Austral zones. It occurs plentifully in the prairie and parkland regions of Saskatchewan and Alberta and appears to be especially abundant in the area of Great Slave Lake. It is known from two localities on the tundra west of Hudson Bay and also occurs in southern Baffin Islands, southern Greenland and Iceland. The characters of *S. vittatum* in all stages are as distinctive as its distribution pattern. It has only one close relative, *Simulium argus* Will., a Cordilleran species occurring from British Columbia to Mexico. *S. vittatum* is extremely adaptable, being found in the largest rivers and the smallest spring-fed streams. It also breeds plentifully at lake-outlets.

Lastly in *Simulium*, there is a residue of two species unplaced subgenerically. One is an arctic species of unknown affinity, *Simulium nigricoxum* Stone. Its immature stages are still undiscovered. It occurs on the tundra, from Alaska to Hudson Bay. The other is an undescribed species, a very close relative of *Simulium pictipes* Hgn. that occurs in the eastern Canadian and Hudsonian zones.

CONCLUSION

The general effect of glaciation appears to have been to concentrate the surviving remnants of the northern fauna into the eastern and western mountain systems and to a lesser extent in the central river basins whence, with the retreat of the ice, they spread with varying success among the groups throughout the enormous river systems flowing into the northern seas. The fact that Prosimuliinae are somewhat more northern in their general distribution than Simuliinae suggests that the family is temperate rather than tropical in origin. Probably this subfamily suffered greater extinction of forms during glaciation than Simuliinae. No Simuliidae have been found in the high arctic. The distribution of one species (*S. vittatum*) gives evidence of a former connection of eastern Canada with Greenland and Iceland at a time when there was no connection in the Bering Strait area. The absence of some and scarcity of other transcontinental species in the Mackenzie valley as far south as the prairies suggests that these species either were never able to become established there or after being established were later eliminated by unfavourable conditions, their place being taken by species with different distributions. There does not seem to be any evidence in the simuliid fauna to support the idea of species surviving in small isolated unglaciated arctic refugia in the central or eastern part of the continent.

REFERENCES

Dyar, H. G., and R. C. Shannon. 1927. The North American two-winged flies of the family Simuliidae. *Proc. U.S. Natl. Mus.* 69: 1–54 (Art. #2636).

Hearle, E. 1932. The black flies of British Columbia (Simuliidae, Diptera). *Proc. Ent. Soc. British Columbia* 29: 5–19.

Hocking, B., and L. R. Pickering. 1954. Observations on the bionomics of some northern species of Simuliidae (Diptera). *Canadian J. Zool.* 32: 99–119.

Hocking, B., and W. R. Richards. 1952. Biology and control of Labrador black flies. (Diptera: Simuliidae). *Bull. Ent. Res.* 43: 237–257.

Nicholson, H. P., and C. E. Mickel. 1950. The black flies of Minnesota (Simuliidae). *Univ. Minnesota Agr. Expt. Sta. Tech. Bull.* 192: 1–64.

Rubtzov, I. A. 1940. Fauna of U.S.S.R. Diptera Vol. VI, No. 6. Simuliidae. *Acad. Sci. U.S.S.R. Moscow.* (Russian with keys and descriptions of new species in English).

Sailer, R. I. 1953. The blackfly problem in Alaska. *Mosquito News* 13: 232–235.

Sommerman, K. M. 1953. Identification of Alaskan black fly larvae (Diptera, Simuliidae). *Proc. Ent. Soc. Washington* 55: 258–273.

Sommerman, K. M., R. I. Sailer, and C. O. Esselbaugh. 1955. Biology of Alaskan black flies (Simuliidae, Diptera). *Ecol. Monogr.* 25: 345–348.

Stone, A. 1952. The Simuliidae of Alaska (Diptera). *Proc. Ent. Soc. Washington* 54: 69–96.

Stone, A., and H. A. Jamnback. 1955. The black flies of New York State (Diptera: Simuliidae). *New York State Mus. Bull.* 349: 1–144.

Twinn, C. R. 1936. The blackflies of eastern Canada (Simuliidae, Diptera). *Canadian J. Res.* (D) 14: 97–150.

DISCUSSION

C. B. Philip. Have you any opinion about the systematic position of the unique *Parasimulium* in northern California? I failed in an attempt to get more specimens in the type locality on Redwood Creek this summer.

G. E. Shewell. I thought it best not to discuss *Parasimulium* in this paper because of an incomplete knowledge of the adults and total lack of information on the immature stages. It seems probable that from the distinctive adult features, a separate subfamily could be maintained for it. I should be very interested to see the type locality.

Distribution Patterns of Northern Fleas (Siphonaptera)[1]

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ABSTRACT

Fleas are ectoparasites of warm-blooded animals, and exhibit various degrees of host-specificity. Some species are restricted to individual species of hosts, while others are associated with groups of hosts, or with certain types of nests. The distribution of fleas in the North today is related partly to the history of the movements of the mammals and birds on which they occur, and partly to other ecological requirements that are not fully known or understood although a number of factors are suggested.

About 67 species and subspecies of fleas are indigenous to the Arctic and Hudsonian regions of the New World, and the distributions of about 50 of these, which are parasitic on terrestrial mammals, are discussed. Although no two geographic ranges are precisely alike, the distributions of Northern fleas may be grouped under six headings as follows: Arctic species (4), amphiberingian species (6), Western subarctic species (8), other Western species (11), transcontinental species (19), and Eastern species (2). Interpretations of the histories of some of the populations are presented, and it is suggested, with host-specific species particularly, that clear-cut affinities between Old and New World fleas may constitute supplementary evidence of value to mammalogists in determining the status of certain species of mammals.

INTRODUCTION

The fleas, or Siphonaptera, are exclusively ectoparasites of mammals and birds. The known world fauna of this small order of insects totals about 1,500 species and subspecies, of which about 67 are indigenous to the "northern" (i.e. Arctic and Hudsonian) regions of the New World; many of them are broadly distributed in the Canadian Zone as well. The 67 northern forms represent seven of the 17 families of Siphonaptera currently recognized (e.g. Hopkins and Rothschild, 1956). They exhibit various degrees of host-specificity, and illustrate a number of distinctive distribution patterns. The preferred hosts of three of the northern forms are mammals of the order Insectivora, while five species are associated with Carnivora, 39 with Rodentia (some of these apparently shared with Insectivora), five with Lagomorpha, one with Chiroptera, and the remaining 14 with birds. The northern bird fleas belong to one family and mostly to one genus, and show close affinities with rodent fleas, from which they undoubtedly were derived.

In the present paper I shall consider mainly about 50 species and subspecies occurring on hosts belonging to the Insectivora, Carnivora, Rodentia, and Lagomorpha, as the fleas that infest bats and birds must have been subjected to somewhat different circumstances in arriving at their present-day distribution because of the volant habits of their hosts; furthermore, records of bird and bat fleas from the North are scanty, and therefore probably unrepresentative.

GENERAL CONSIDERATIONS

In many cases, the geographic distribution of a species of flea coincides approximately with that of a species of mammal on which the flea is regularly found. Sometimes such fleas are known only from one species of host, which is then clearly the "true host", but more often, fleas are also collected on other species of mammals, sometimes closely related ones that occur in the same area. Two interpretations of the latter situation appear possible: (a) that the flea is physically and/or physiologically associated with one species of host (by specific blood-meal requirements, for example), records from the others resulting from accidental or temporary associations that do not permit breeding of the flea, or (b) that flea and host depend on similar or associated ecological requirements so that ranges coincide, although within those ranges, some other hosts are satisfactory. However, few investigations on the ecology or physiology of fleas have been undertaken so that, in the absence of firm data, explanations of present-day distributions and host-relationships are largely based on circumstantial evidence. Students of fleas tend to arrive at opinions that certain species of mammals are the true hosts, and that certain fleas are either restrictive or catholic in their host-requirements, the usual basis being the relative frequency with which a flea is collected on various hosts or in their nests. Fleas believed to be true parasites of one species of host are often found on the natural predators of that host; they may also be found on other mammals that live in close association with the host by using its burrow or runway. Such records, especially those where the alternative hosts are very different (e.g., a mouse-flea, collected on a shrew, or a weasel) may be representative of temporary situations, and it is frequently supposed, though not proved, that such stray fleas die without breeding on the accidental host. There are some species, however, such as all the bird fleas, that must have developed from populations that *did* effect a successful transfer on a permanent basis.

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More difficult to interpret are occurrences of fleas on closely related hosts. For instance, mice of the genera *Microtus*, *Clethrionomys*, *Synaptomys*, and *Phenacomys*, living in close association, are often infested with the same species of fleas, and in many cases it seems probable that the insects are able to breed successfully in the nests of each species of host. Even supposing this, however, and in spite of numerous confusing records, I believe that a fundamental relationship or history of association may often be traced between a species of flea and a species of mammal.

Some species of fleas that appear to have a strong affinity for a particular species of mammal do not occupy the entire geographic range of that mammal, and they may or may not be replaced by other species in other parts of the range of the mammal. In all such cases, even supposing a physiological association between flea and mammal, we must search for other reasons that will explain the restricted distribution. Here again, only speculation is possible at this time, there being no measured data available.

Following is a brief list of some factors that must influence the distribution of fleas. Some of these relate especially to the host, others to other aspects of the environment. They represent a virtually untouched field for research.

1. Reproductive potential of the species.
2. Specificity of blood mean requirements (not only species of host, but also age and sex of host).
3. Skin thickness of host in relation to mouthparts of flea (accessibility of blood supply).
4. Pelage of host from standpoint of heat insulation.
5. Vestiture of flea in relation to pilosity of host (physical security of flea as it moves about on the animal).
6. Habits and activities of the host (e.g. species of mammals that are strongly aquatic, such as the otter, beaver, and muskrat, are ordinarily free of fleas, probably for this reason, while non-aquatic mammals, especially those that regularly use dens or nests, usually have fleas).
7. Presence of essential food ingredients for flea larvae in nest of host.
8. Ranges of temperature, humidity and light in nest of host in relation to tolerances of flea eggs, larvae, and pupae (and adults, especially in the case of "nest fleas").
9. Timing of life-history stages of the flea in relation to the occupancy, and eventually to the abandoning of nest by the host.
10. Longevity of adult fleas on host in relation to breeding intervals of host, especially hosts that do not repeatedly use the same sleeping site.
11. Presence of parasites, predators, or diseases, attacking any stage of the flea or host. (The host itself is sometimes a predator, or at least a voluntary or involuntary destroyer of fleas).
12. Host-finding capacities of adult fleas.
13. Time.

The relative breadth or narrowness of the tolerances of fleas to these and other factors will determine their success, in competition with other species, in occupying all or part of the range of a suitable host or hosts.

A number of authors (e.g. Wagner, 1936; Jellison and Kohls, 1939; Holland, 1949, 1950a) have drawn attention to the close affinity between the flea fauna of north-western America, and that of eastern Asia. Recent studies based on extensive northern collections have emphasized the closeness of this relationship. Although, unfortunately, there have been few opportunities for making actual comparisons of specimens from the Palaearctic and Nearctic Regions, both Old World and New World students of fleas, working mainly from the literature, have nevertheless given serious consideration to this question so that more and more species names have been sunk in synonymy, or at least reduced to subspecific status.

I consider 19 of the 50 Nearctic forms under principal consideration to occur also in the Palaearctic Region, sometimes as subspecies, and 24 others to belong to genera that are well represented in the Old World. The remaining few are distinctly Nearctic, and most, though not all, infest hosts that have no very close relatives in the Old World. The 50 Nearctic fleas represent 24 genera of which only six are not known also from the Old World[3]. However, before examining their distributions in detail, let us first consider something of the history and taxonomic status of the mammals on which fleas occur.

Simpson (1947), considering the fossil record on mammalian faunal relationships from the Eocene to the present, found no evidence of Atlantic migration routes. On the other hand he concluded major faunal interchanges across a Bering bridge between "Alaska" and "Siberia" during early Eocene, late Eocene, early Oligocene, late Miocene, middle to late Pliocene, and Pleistocene, with weak interchange during several other intervals of the Cenozoic. He stated, too, that the Bering land connection persisted throughout the early and middle Pleistocene. He presumed that the actual migrations (either way) were mainly interglacial and that the migrants advanced southward and spread out on each continent, with widespread effects on the whole continental faunas, especially during the glacial stages.

According to the available fossil evidence, the genera of the principal flea-bearing mammals of the North arose at various times from the Lower Miocene to the Pleistocene, appearing first sometimes in North America, sometimes in Europe or Asia, or in the Old and New Worlds simultaneously. The directions of movement during the ensuing periods are in general indefinite, and the history of the parasites of the mammals during their long history of evolution and geographic radiation is difficult if not impossible to reconstruct in detail. As mentioned earlier, the fleas now occurring in the northern parts of the Nearctic and Palaearctic bear varying degrees of similarity to each other. It may be supposed that those species or subspecies exhibiting the closest resemblance usually represent the most recent faunal contacts, whereas increased degrees of difference imply more ancient relationships, and refer back to earlier contacts between the faunas of the New and Old Worlds. Similarly pairs of species in the New World are, in some cases, extremely similar, suggesting that the geographical isolation of their progenitors was relatively recent, while others, though sufficiently alike to indicate a common ancestry, have diverged to a degree that suggests the passage of a very long period of time. These facts appear to be quite in keeping with the now accepted history of a succession of contacts between the faunas of the Old and New Worlds and a series of major glacial periods in northern North America since the onset of the Pleistocene.

According to Flint (1952) the Pleistocene epoch probably occupied a million years, and involved four glacial periods punctuated by lengthy inter-glacial periods. During the height of the last glacial period, mammals (and fleas) were undoubtedly eliminated from most of the northern part of North America (e.g. Hibbard, 1949). Repopulation of what are now Canada and Alaska has come in part through reinvasions from areas that lay to the south of the Cordilleran and Laurentide ice sheets, and in part from unglaciated refugia that persisted throughout the Pleistocene, and of which the most important was apparently the Beringian refugium which included a large section of Alaska and Yukon as well as parts of eastern Siberia, and of course the Bering Straits region itself which has acted as a "land bridge" on a number of occasions. Present day distribution patterns of mammals, and from the flea-standpoint, of small mammals especially, support this thesis. The resemblance between the northern mammalian faunas in the Palaearctic and Nearctic is striking and significant. A number of mammalogists (e.g. Rausch, 1950, 1953) now consider many mammals to be conspecific in the two regions. At the present time, for example, the grizzly and big brown bears (*Ursus arctos* L.), red and arctic foxes (*Vulpes vulpes* L. and *Alopex lagopus* L.), ermine (*Mustela erminea* L.), wolverine (*Gulo gulo* L.), lynx (*Felis lynx* L.), arctic hare (*Lepus timidus* L.), hoary marmot (*Marmota marmota* L.), Arctic ground squirrel (*Citellus undulatus* Pallas), brown and collared lemmings (*Lemmus sibiricus* Kerr and *Dicrostonyx torquatus* Pallas), red-backed voles (*Clethrionomys rutilus* (Pallas)) and tundra voles (*Microtus oeconomus* Pallas) have been stated to be Holarctic, or at least amphiberingian species, and the possibility that the shrew *Sorex tundrensis* Merriam, least weasel *Mustela rixosa* Bangs, and the collared pika *Ochotona collaris* Nelson are conspecific with the Palaearctic *Sorex araneus* L., *Mustela nivalis* L., and *Ochotona hyperborea* Pallas, has been suggested. The close relationships between these Old and New World mammals are frequently reflected in their fleas.

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[3] Actually there are more than 18 Holarctic genera of fleas and some of these (e.g. *Pulex*, *Atyphloceras*, *Stenoponia*, *Neopsylla*. *Ctenophthalmus*, *Geusibia*, *Odontopsyllus*, and *Diamanus*) are represented, sometimes by closely related species, in the Old and New Worlds, but not in the northern regions.

Rand (1954) discussed six types of distribution patterns of Nearctic Mammalia, each illustrating presumed histories of geographic isolation with subsequent evolutionary diversification of species, and based upon the relationships of a number of refugia. He cited a number of pairs or threes of closely similar species that are allopatric or partially sympatric today, and that he believed to be of common ancestry, but descended from populations that were separated and isolated from each other for periods sufficient for genetic discontinuity to become complete. In a number of cases, the fleas of such pairs of mammals also occur in pairs, and appear to support Rand's contention. In other cases, one of the mammals of such a pair may possess a flea or fleas not represented on its "opposite number". In some of these cases we may speculate that the missing fleas were not represented on the populations of mammals that became isolated, or that if they were, they have since become extinct.

Supposing then, that fleas became isolated with their hosts during the glacial periods, and especially during the height of the last, or Wisconsin, glaciation there is evidence that the parasites were not always able to radiate from the residual areas simultaneously with their hosts upon the recession of the ice sheets. A striking example is provided by some fleas of the genus *Atyphloceras*. *Atyphloceras bishopi* Jord., was described from the Adirondacks, N.Y., where it occurs principally on the common meadow mouse, *Microtus pennsylvanicus*, an extremely widely distributed mammal. However, *A. bishopi* occurs in only a small part of the range of *M. pennsylvanicus* in eastern North America. The most northwesterly record is from Cochrane, Ontario. The closest relative of *A. bishopi* is *A. nuperus* Jord., which is known only from the Dolomites and other mountainous areas of central and southern Europe, where it occurs on microtines. No similar flea is known from other parts of Europe or of Asia (*A. shogakii* Jam. and Sakag. of Japan being very different) and the other Nearctic species of *Atyphloceras*, all western, are not closely allied to *bishopi* and *nuperus*. We may suppose, then, that *Atyphloceras* spp. of the *bishopi-nuperus* group in past ages were represented across the breadth of Eurasia and North America but that only the ends of the chain now exist, and these are now prevented by undetermined factors from reinvading the old range.

In other cases, fleas appear to have moved northward with their hosts, but to have become extinct in more southerly areas still occupied by those same hosts; or, conversely, we might suggest that the hosts have moved south from a subarctic habitat, but the fleas have not moved south with them. Still other species of fleas have developed immense territorial ranges in the Canadian, Hudsonian and southern Arctic Regions where they may infest hosts of several families and even orders.

Although no two species of fleas appear to have precisely the same distribution, the ranges of the "northern" fleas of the New World may be conveniently considered under six major headings. In the space available, it will not be possible to discuss the range of each species in detail. However, I propose to deal with each major distribution pattern in a general way, selecting several species for illustration. Distribution maps of mammals are adapted from Burt and Grossenheider (1952). Records of fleas are based almost entirely upon specimens preserved in the Canadian National Collection of Insects, Ottawa. A few United States records are selected, mainly from Hubbard (1947).

ARCTIC SPECIES

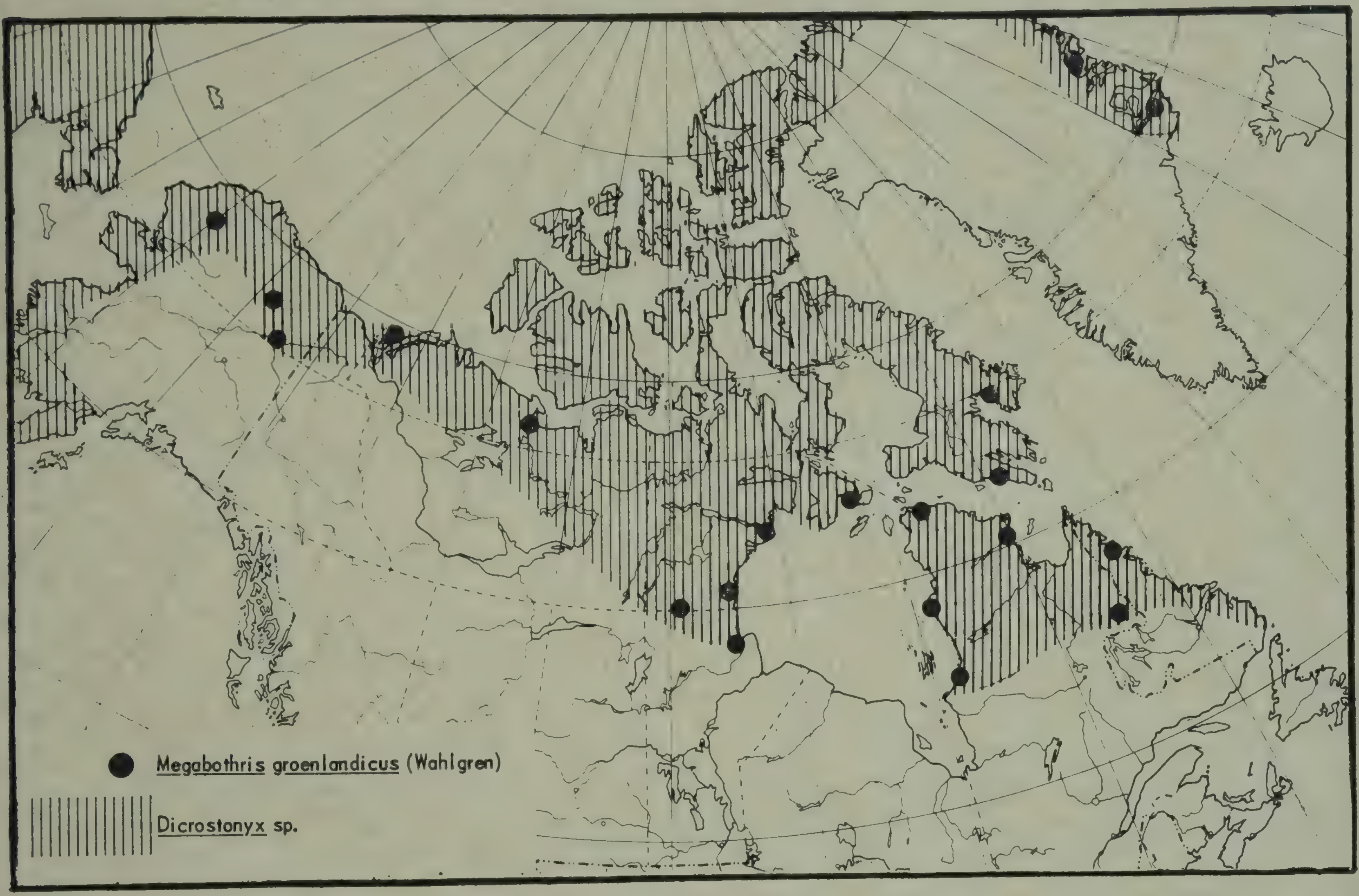
Hoplopsyllus glacialis glacialis (Taschenberg) on Arctic hares, *Lepus arcticus* group (or *Lepus timidus* L.);

Megabothris groenlandicus (Wahlgren) on lemmings, *Dicrostonyx* and *Lemmus* spp.;

Ceratophyllus lunatus tundrensis Holland on weasels, *Mustela erminea* ssp.;

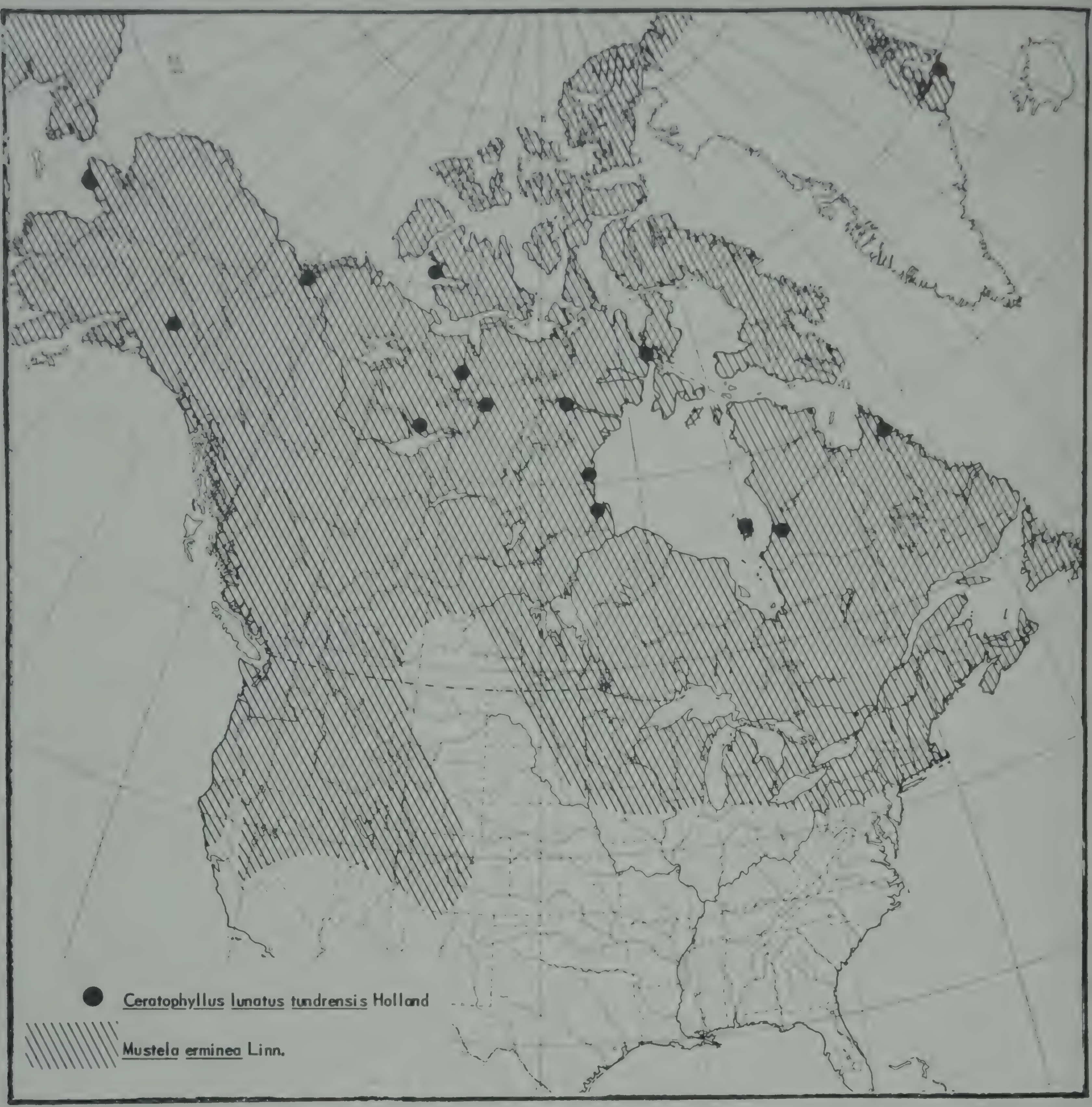
Oropsylla alaskensis (Baker) on ground squirrels, *Citellus undulatus* ssp.;

The four species of fleas listed are true barren land species, and apparently occur throughout those areas of the tundra inhabited by their hosts. Their ranges tend to be Low rather than High Arctic. The first three species occur in Greenland as well as in Canada and Alaska. All but one species (and possibly that one) occur also in the Palaearctic Region. None of them, so far as is known, occurs in Arctic-Alpine areas of the mountains of Canada or the United States.



The lemming flea, *M. groenlandicus*, occurs on the collared lemming *Dicrostonyx* sp. from Greenland to St. Matthew Island, Alaska, and as far south as Churchill, Manitoba (Fig. 1). Within the range of *Dicrostonyx*, it occurs also on the brown lemming *Lemmus* sp., and occasionally on *Microtus* spp., but apparently not elsewhere. Curiously enough it has never been reported from the Palaearctic Region where both genera and allegedly the same species of lemmings occur. It is possible that *Megabothris advenarius* (Wagner), of northeastern Asia, is a Palaearctic representative of *M. groenlandicus;* published illustrations suggest that it is close, though not conspecific with *groenlandicus*. In parts of the Palaearctic, the common lemming flea appears to be *Megabothris rectangulatus* (Wahlgren) which is not known from the New World. Unlike *M. groenlandicus*, *M. rectangulatus* has been recorded from some areas (Scotland and Switzerland, for example) where lemmings do not, or do not now occur. Aside from *M. advenarius*, the nearest known relatives of *M. groenlandicus* are two Nearctic species, *M. quirini*, which has a Hudsonian and Canadian distribution on a number of Microtinae and Zapodidae, and *M. lucifer* (Rothschild), a species of southwestern Canada; *M. rectangulatus* is not especially closely related, although it is superficially similar.

Ceratophyllus lunatus Jordan and Rothschild was described from Switzerland where it apparently occurs as a relict , on weasels, *Mustela* sp. *C. l. tundrensis* occurs from Greenland to Alaska, on weasels, *Mustela erminea* (Fig. 2). The species is also known from Kamchatka and other parts of eastern Asia, and published figures suggest that the form



there is more closely akin to *tundrensis* than to the nominate subspecies. It is interesting to note that *Mustela erminea* is broadly distributed in north temperate regions as well, but *C. l. tundrensis* occurs only on Arctic populations.

Oropsylla alaskensis occurs in the truly Arctic portions (the northern and eastern parts) of the range of the Parry ground squirrel, *Citellus undulatus* ssp. (=*C. parryi* ssp.) including St. Lawrence Island, Alaska; this ground squirrel is infested by other species of fleas in other parts of its range, especially in areas that are Subarctic rather than Arctic. Like *Ceratophyllus l. tundrensis*, it apparently provides an example of dependence of the flea upon other ecological factors than the mere presence of a particular host. The validity of this surmise, of course, depends upon the ultimate evaluation of the northern "races" of ground squirrels by the mammalogists, a matter of some controversy at the present time. One record of *O. alaskensis* from Craig Harbour, Ellesmere Island, is far removed from the known range of *Citellus*. The specimens were taken from Arctic fox, *Alopex lagopus* ssp., and probably indicate the widely ranging habits of this carnivore. Ioff and Scalon (1954) consider *O. asiaticus* Wagner, a parasite of *Citellus undulatus* in Kamchatka, Mangolia, Manchuria, and other parts of eastern Asia to be a synonym of *O. alaskensis*.

AMPHIBERINGIAN SPECIES

Catallagia dacenkoi fulleri Holland, and *Malaraeus penicilliger dissimilis* Jordan on red-backed mice, *Clethrionomys rutilus* ssp. (=*C. dawsoni* ssp.);

Peromyscopsylla ostsibirica longiloba (Jordan), and *Megabothris calcarifer gregsoni* Holland on tundra mice, *Microtus oeconomus* ssp., (=*M. operarius* ssp.);

Amphipsylla marikovskii ewingi Fox on mice, *Microtus* spp.;

Monopsyllus tolli (Wagner) on pikas, *Ochotona collaris* (Nelson).

The six species of fleas listed are represented on equivalent hosts in eastern Siberia and northwestern North America. The Nearctic "subspecies" are sometimes assumed rather than proved. The Nearctic distribution of these fleas radiates around a large area of Alaska and Yukon that was not glaciated during the Pleistocene, and it seems probable that the fleas have stemmed from a residual fauna that survived in this refugium. In any case a Northwestern origin seems indicated as the closest relatives of all these fleas are Palaearctic rather than Nearctic.

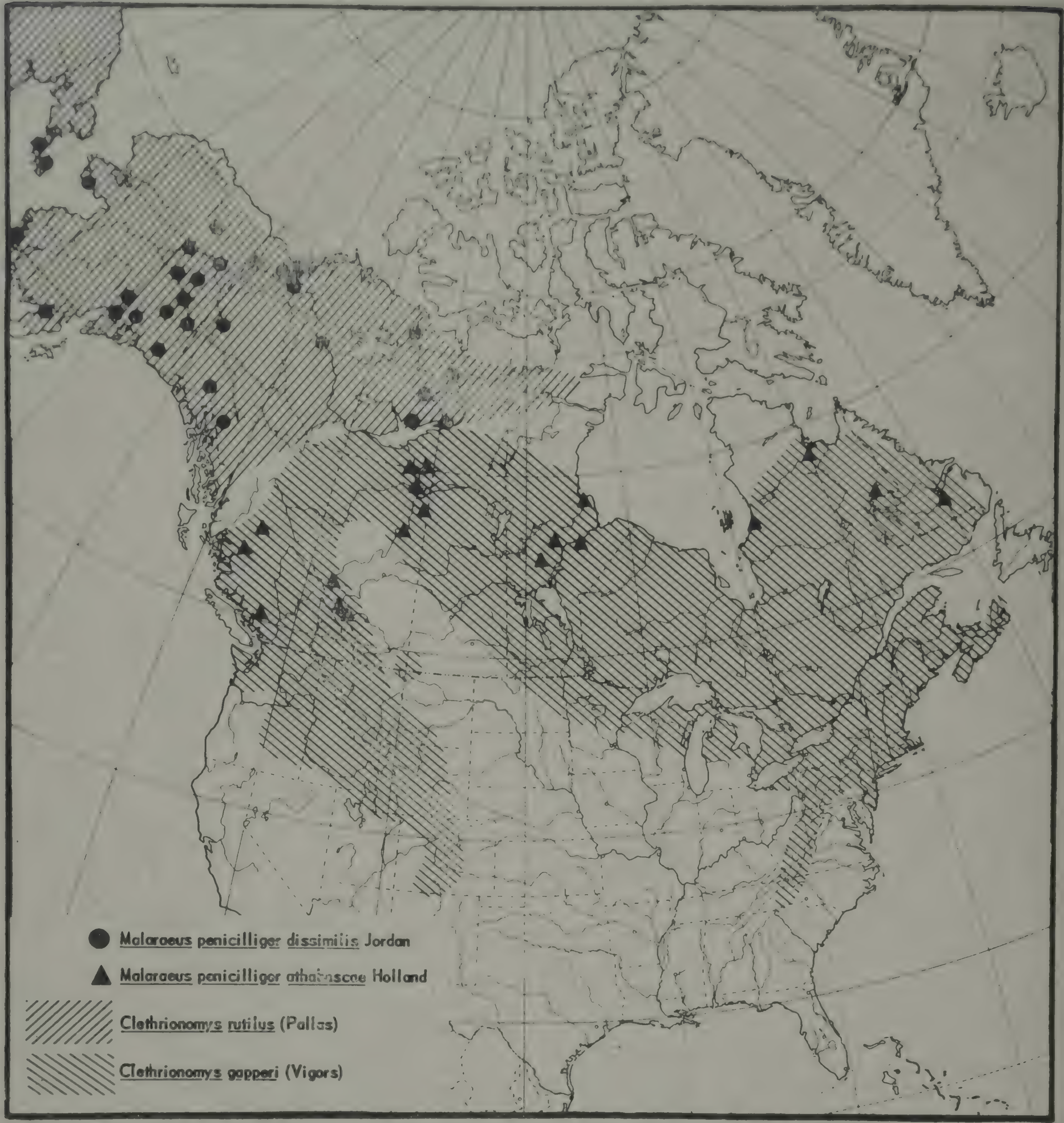
Their present ranges differ in detail, even when they occur on the same hosts, and this may reflect differences in the ability of the various species to tolerate changing marginal conditions following the recession of the glaciers. Five of the species are mouse fleas, and occur principally on *Microtus oeconomus* Pallas and *Clethrionomys rutilus* (Pallas) which are believed by Rausch (1950) and others to be amphiberingian species.

Of the fleas assumed to have stemmed from Beringia, *Peromyscopsylla ostsibirica longiloba* is perhaps the most striking. Its known distribution today corresponds fairly closely to the area believed not to have been glaciated, although its hosts (microtines, especially *Microtus oeconomus*) now have distributions extending considerably beyond this area. It is barely distinguishable, if at all, from *P. o. ostsibirica* (Scalon) of Siberia. Its closest relative in the New World, *P. hamifer* (Rothschild), is abundantly distinct, as is *P. bidentata* (Kolenati) of the Old World. *Amphipsylla marikovskii ewingi*, of which only a few records are available, appears to have a similarly restricted distribution.

Microtus oeconomus and *Clethrionomys rutilus* form with *M. pennsylvanicus* Ord. and *C. gapperi* (Vigors) two of the pairs of species of mammals that Rand (1954) believes to have a primordial common ancestry although they are specifically distinct today, following the breakdown of geographical barriers so that their ranges are now in contact; in the case of *M. oeconomus* and *M. pennsylvanicus*, there is now extensive overlap of broad geographic range, although the species may be ecologically isolated locally (e.g. Cameron, 1952). Just how long ago was the initial segregation of northern and southern populations is difficult to postulate, but the presence on these mice of corresponding pairs of fleas that are well characterized taxonomically, though obviously closely akin, suggests that they were not among the more recent evolutionary products of the Pleistocene.

M. oeconomus is parasitized through most of its range by *Megabothris calcarifer gregsoni* and through part of its range by *Peromyscopsylla ostsibirica longiloba*, while *M. pennsylvanicus* carries the complementary species *Megabothris asio* (Baker) (two subspecies, one eastern and one western) and *Peromyscopsylla hamifer* (also two subspecies). In the overlapping area, *M. pennsylvanicus* is sometimes infested with *Megabothris calcarifer* as well as with *M. asio*. Recent collections of *M. asio megacolpus* Jord. and *M. calcarifer gregsoni* from the same locality and the same species of host (Aklavik N.W.T., ex *Microtus pennsylvanicus*) substantiate the decision (Holland 1950b) to recognize the two forms as species rather than as subspecies.

The Holarctic mouse *Clethrionomys rutilus* carries a flea *Malaraeus penicilliger dissimilis* apparently throughout its range in North America (Fig. 3). The subspecies *dissimilis* was recently reported from Kamchatka (Ioff and Scalon, 1954) and several other subspecies or representatives of *M. penicilliger* (Grube) occur in the Palaearctic Region, mostly on *Clethrionomys* spp. Roughly south of Great Slave Lake in Canada, *Clethrionomys rutilus* is replaced by *C. gapperi* which ranges widely across most of the forested areas of Canada, and extends well into the United States. In the Hudsonian part of its range only, *C. gapperi* is parasitized by a flea described as *Malaraeus penicilliger athabascae*, although it is so well characterized it probably should be considered a full species. *M. p. athabascae* is distributed transcontinentally through the Hudsonian Zone as far as Goose Bay, Labrador; in the west, it extends southward in the Cordillera to Tenquille Lake in the Coast Range, and to Banff in the Rockies. No other close relative of *M. penicilliger* is known from *Clethrionomys* in North America. It seems probable that *M. p. athabascae* is only able to tolerate relatively Subarctic conditions, so that while it spread northward on its host


● Malaraeus penicilliger dissimilis Jordan
▲ Malaraeus penicilliger athabascae Holland
▨ Clethrionomys rutilus (Pallas)
▨ Clethrionomys gapperi (Vigors)

upon the recession of the ice, it was not able to persist in the areas to the south when the climate moderated or when it competed with better adapted species, although the host has been able to subsist satisfactorily.

Catallagia dacenkoi Ioff is broadly distributed (Altai, Transbaikalia, Mongolia, etc.) in eastern Asia. Its New World representative, *C. dacenkoi fulleri* has been recorded from *Microtus* spp., but seems to be associated more usually with *Clethrionomys* spp; it occurs on northwestern populations of *C. gapperi* as well as on *C. rutilus*.

WESTERN SUBARCTIC SPECIES

Chaetopsylla tuberculaticeps ursi (Rothschild) on grizzly and big brown bears, *Ursus arctos* group;

Catallagia jellisoni Holland, and *Amphipsylla sibirica pollionis* (Rothschild) on mice, Microtinae;

Malaraeus penicilliger athabascae Holland on red-backed mice, *Clethrionomys gapperi* ssp.;

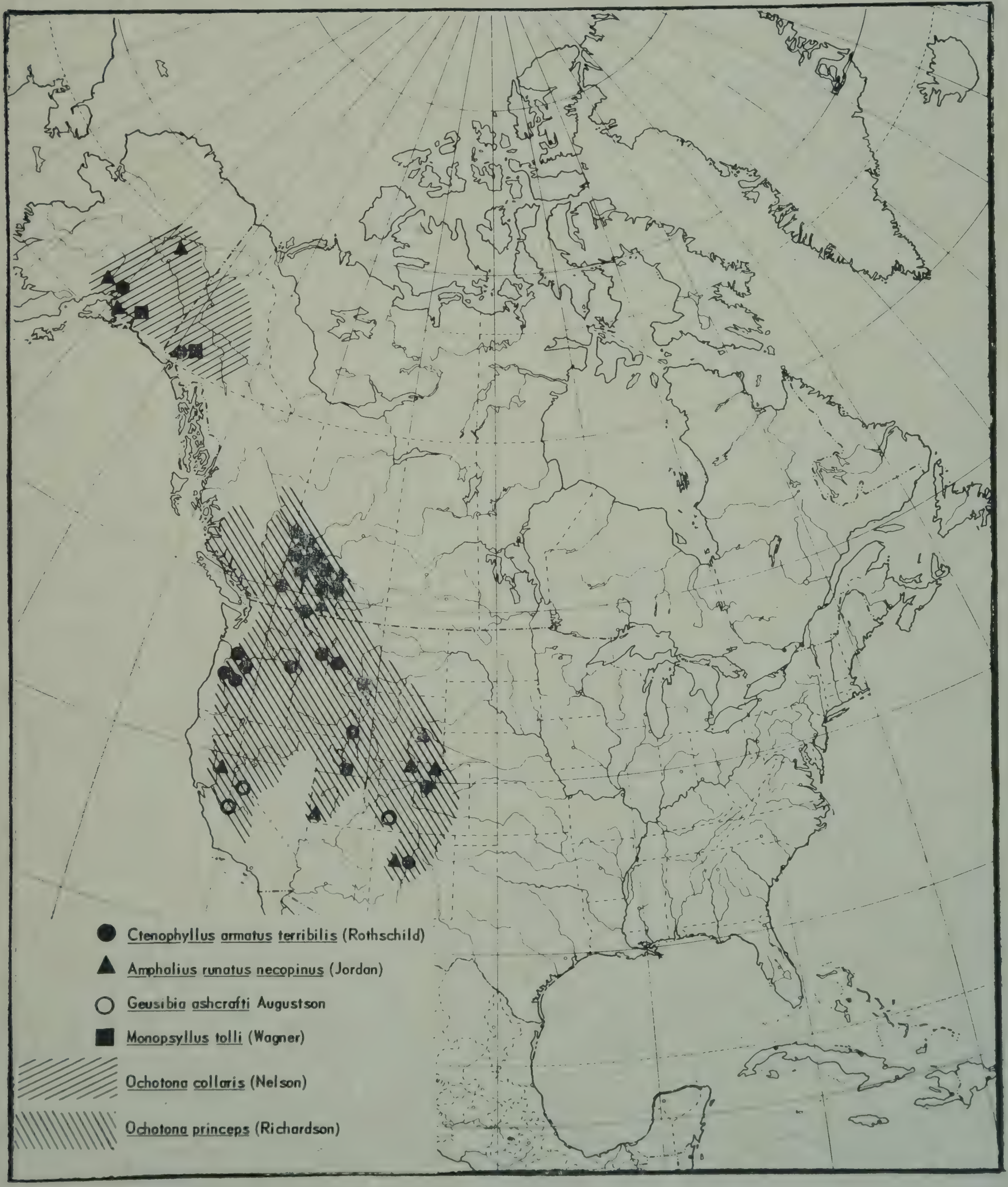
Ctenophyllus armatus terribilis (Rothschild), and *Amphalius runatus necopinus* (Jordan) on pikas, *Ochotona* spp.;

Tarsopsylla octodecimdentata coloradensis (Baker) on arboreal Sciuridae (*Tamiasciurus* and *Glaucomys* spp.);

Oropsylla idahoensis bertholfi (Fox) on ground squirrels, *Citellus undulatus* spp.

The eight species of fleas listed are distributed across much of the northwestern part of the Continent, but extend southwards along the Cordillera, some of them as far as California. A few range rather far east in the Hudsonian Zone as well. All of these species have extremely close relatives in the Palaearctic Region; in fact, there is the strong likelihood that all the species are Holarctic, although this is not yet reflected in the nomenclature in one or two cases. These species, or some of them, may have (a) survived the glaciations in Beringia and spread south (and sometimes east) in post-Pleistocene times (b) survived in a southwestern montane refugium and spread north on the retreat of the ice, or (c) survived as northern *and* southern residual populations which, though isolated for long periods, have not diverged to a point where morphological differences can be detected, although the host animals may have evolved to the point where they are now *considered* separate species. The third possibility seems the most likely in some of the cases, and seems to be rather strongly suggested in the case of the pika fleas (Fig. 4).

Pikas, *Ochotona* spp., occur over much of the eastern part of the Palaearctic where they live in rocky talus slopes in the mountains. They occur in similar habitats in the Cor-


● Ctenophyllus armatus terribilis (Rothschild)
▲ Amphalius runatus necopinus (Jordan)
○ Geusibia ashcrafti Augustson
■ Monopsyllus tolli (Wagner)
Ochotona collaris (Nelson)
Ochotona princeps (Richardson)

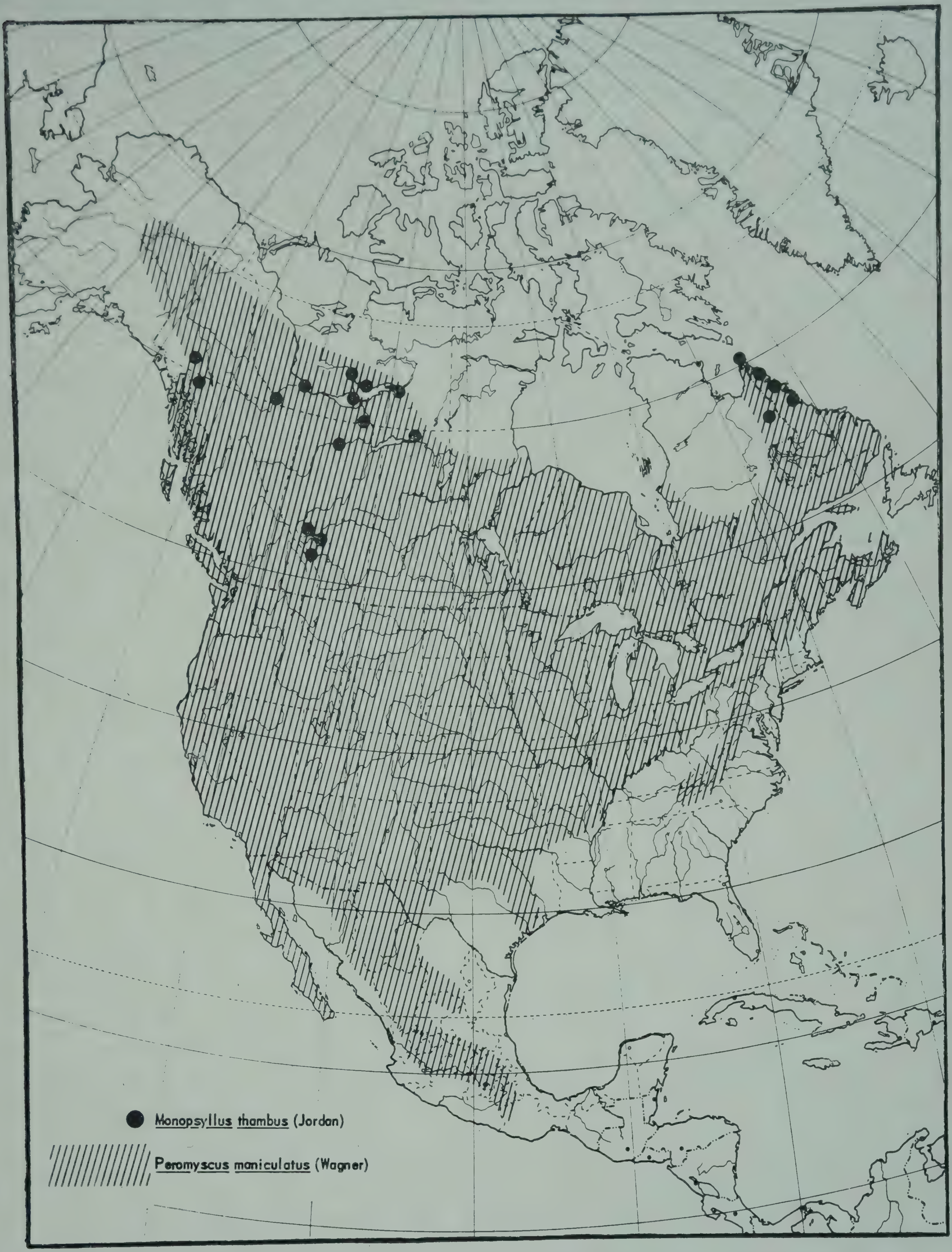
dillera from Alaska and Yukon to Colorado and California. The Alaskan pika, *Ochotona collaris* (Nelson) has been considered specifically distinct from the Rocky Mountain pika, *O. princeps* (Richardson), and the two are regarded by Munro and Cowan (1947) as the descendants of northern and southern residual populations respectively. The two species remain widely separated today although it is perhaps not safe to assume that this separation has been continuous since the last glaciation. Pikas possess a number of highly host-specific fleas of which the larger number of genera and species occur in the Old World, where twelve species of *Ochotona* are recognized, suggesting that the pikas themselves originally stemmed from this source. However, four species of fleas belonging to four Holarctic genera are known from Nearctic *Ochotona* spp. One, *Geusibia ashcrafti* Augustson, is known only from California and Colorado; the only other species of the genus, *G. torosa* Jord., occurs in China. *Monopsyllus tolli*, described from Siberia, has recently been collected from pikas (*O. collaris*) in Yukon (Holland, 1952) and Alaska, but is not known elsewhere from North America. On the other hand, *Ctenophyllus terribilis* and *Amphalius necopinus* are known from both the Alaskan and the Rocky Mountain pikas. Northern and southern specimens appear to be indistinguishable; furthermore they are hardly separable from *Ctenophyllus armatus* (Wagner) and *Amphalius runatus* (Jordan) of the Old World; at the most they should be considered as subspecies of the latter. I suggest then that the New World pikas were indeed separated into northern and southern populations during the glaciations; that the representatives of *Ctenophyllus* and *Amphalius* have remained apparently unchanged during the period that has elapsed; and that northern representatives of *Geusibia* may have become extinct as may have southern ones of *Monopsyllus tolli*, if indeed the latter ever occurred on the southern pikas.

A somewhat similar situation occurs in the case of *Oropsylla idahoensis* (Baker), a flea of western ground squirrels. It occurs throughout most of the range of *Citellus columbianus* (Ord) in the Rocky Mountains, and a weak subspecies, *O. idahoensis bertholfi* occurs on populations of *Citellus undulatus* in Northern British Columbia and western Alaska. The ranges of *Citellus undulatus* and *C. columbianus* are not now in contact, and they may not have been, since prior to the last glaciation. *O. idahoensis* is close to the Asiatic *O. ilovaiskii* Wagner and Ioff and may be conspecific with it.

Rausch (1953) stated that the North American grizzlies and big brown bears should be considered no more than subspecies of the Palaearctic *Ursus arctos* L. A flea, *Chaetopsylla tuberculaticeps* (Bezzi) occurs on these bears in the Old and New Worlds; in the Nearctic Region, where it is known as *C. tuberculaticeps ursi* (Rothschild), this flea occurs from Alaska southwards along the Cordillera at least to Montana.

Amphipsylla sibirica (Wagner) is a polytypic species that parasitizes Microtinae through central Europe, Lapland, the Ural and Tyan-Shan mountains, Siberia, and North America. Five subspecies are currently recognized from the Palaearctic Region and two have been described from the New World, although I feel that one of these, *A. s. washingtona* Hubbard, should be considered a full species. However, *Amphipsylla sibirica pollionis* occurs in Alaska and Yukon, and extends southward along the Rocky Mountains at least to Banff; it infests Microtinae, chiefly of the genera *Microtus* and *Clethrionomys*. Although it has not been collected across north-central Canada, a population, apparently indistinguishable, was discovered recently in Northern Labrador. Whether this illustrates a true disjunct distribution, or merely indicates poor collecting, is difficult to say. An almost precisely similar situation occurs with the strictly Nearctic species *Monopsyllus thambus* which occurs on the Nearctic mouse *Peromyscus maniculatus* ssp. in western Subarctic localities, extending down the Rockies to Banff, and then turns up again at the northern tip of Labrador and adjacent parts of Quebec (Fig. 5). Deevey (1949) warns against the assumption that disjunct distributions are necessarily old, and points out that the habitat occupied by the disjuncts may more usually be the one in which they have a competitive advantage over more widely distributed species. One might speculate, then, that there was a continuous population of *thambus* at an earlier stage in the last postglacial, but that more southerly populations were eliminated by competition with more successful species[4] which, however, were not able to penetrate to the most northern parts of the range of the mouse (occupied by *thambus*) so that an east-west separation became effected.

[4] e.g. *Orchopeas leucopus* (Baker) in the east and *Monopsyllus wagneri* (Baker) in the west, which are the dominant fleas of *Peromyscus maniculatus* over much of its range, but scarce or absent from areas occupied by *thambus*.


● Monopsyllus thambus (Jordan)
▨ Peromyscus maniculatus (Wagner)

Catallagia jellisoni, known at present only from Atlin, B.C. and Banff, Alberta, is extremely similar to *C. fetisovi* Vovchinskaya and *C. ioffi* Scalon of eastern parts of the U.S.S.R. and Mongolia, and may be a subspecies of one of these. It probably has a continuous distribution between the two localities from which it is known at present.

Tarsopsylla coloradensis, which is known from western North America from Alaska to New Mexico has been reduced to the status of a subspecies of the Old World *T. octodecimdentata* (Kolenati) by Smit (1953); it is associated with genera of Sciuridae that are not known from the Palaearctic Region.

OTHER WESTERN SPECIES

Nearctopsylla brooksi (Rothschild) on weasels, *Mustela* spp.;
Nearctopsylla hyrtaci (Rothschild) on shrews, *Sorex* spp.;

Hystrichopsylla occidentalis Holland on Rodentia and Insectivora;

Catallagia charlottensis (Baker), and *Catallagia decipiens* Rothschild on white-footed mice, *Peromyscus* spp.;

Megabothris abantis (Rothschild) on Microtinae;

Monopsyllus ciliatus protinus (Jordan) on red squirrels, *Tamiasciurus* spp.;

Delotelis hollandi Smit on Microtinae;

Orchopeas sexdentatus ssp. on woodrats, *Neotoma cinerea* ssp.;

Opisodasys keeni (Baker) on white-footed mice, *Peromyscus* spp.;

Thrassis spenceri Wagner on hoary marmots, *Marmota marmota* ssp. (= *M. caligata* ssp.).

About eleven species of fleas have a Canadian and Hudsonian distribution in the Cordilleran region, most of them ranging from the Rocky Mountains westward to the Pacific Coast, where some of them occur also on the islands. The first seven species listed belong to Holarctic genera, but do not have any very close relatives in the Palaearctic Region. Several of them are associated with genera and families rather than with species of hosts. The remaining four species belong to strictly Nearctic genera. All of the species are probably "southern" in origin in so far as post-Pleistocene repopulation of the northern areas is concerned. One of the species (*Monopsyllus ciliatus*) is restricted to the Pacific Coast strip including the islands, wherever its host *Tamiasciurus* spp., occurs. *Catallagia charlottensis* is largely coastal too, but extends part way into the interior, in moist localities.

Megabothris abantis is interesting in that it occurs on many species of mice as well as on several other hosts, but is evidently restricted to areas from the Rocky Mountains westward. Although several of the mammals on which *Megabothris abantis* is common are much more widely distributed than the flea, one of the mice on which it is regularly found, *Microtus longicaudus* (Merriam), has roughly the same range; it is possible that some correlation exists. The distribution and host-relationships of *Hystrichopsylla occidentalis* and *Delotelis hollandi* appear to be rather similar so far as can be judged from the limited number of records available.

Although *Thrassis spenceri* is undoubtedly a true parasite of the hoary marmots, which Rausch (1953) states are conspecific with the Palaearctic *Marmota marmota*, it appears that the genus *Thrassis* is not known from the Old World. H. E. Stark of California has discovered a number of entities (species? subspecies?) of the *spenceri*-group from isolated "species" of alpine marmots.

TRANSCONTINENTAL SPECIES

Hoplopsyllus glacialis lynx (Baker) on varying hares, *Lepus americanus* group;

Corrodopsylla curvata curvata (Rothschild) on shrews, *Sorex* spp.;

Rhadinopsylla fraterna fraterna (Baker) on many Rodentia;

Peromyscopsylla selenis (Rothschild) on Microtinae;

Peromyscopsylla hamifer hamifer (Rothschild), and *Megabothris asio* (Baker) (two subspecies) on meadow mice, *Microtus pennsylvanicus* (Ord);

Megabothris atrox (Jordan) on weasels, *Mustela* spp.;

Megabothris quirini (Rothschild) on Microtinae and Zapodidae.;

Monopsyllus vison (Baker) on red squirrels, *Tamiasciurus hudsonicus* ssp.;

Monopsyllus eumolpi (Rothschild) on western chipmunks, *Eutamias* spp.;

Monopsyllus wagneri systaltus (Jordan), and *Monopsyllus thambus* (Jordan) on white-footed mice, *Peromyscus maniculatus* ssp.;

Oropsylla arctomys (Baker) on woodchucks, *Marmota monax* ssp.;

Oropsylla rupestris (Jordan) on ground squirrels, *Citellus* spp.;

Epitedia wenmanni wenmanni (Rothschild), and *Orchopeas leucopus* (Baker) on mice, especially *Peromyscus* spp.;

Orchopeas caedens (Jordan) (two subspecies) on red squirrels, *Tamiasciurus hudsonicus* ssp.;

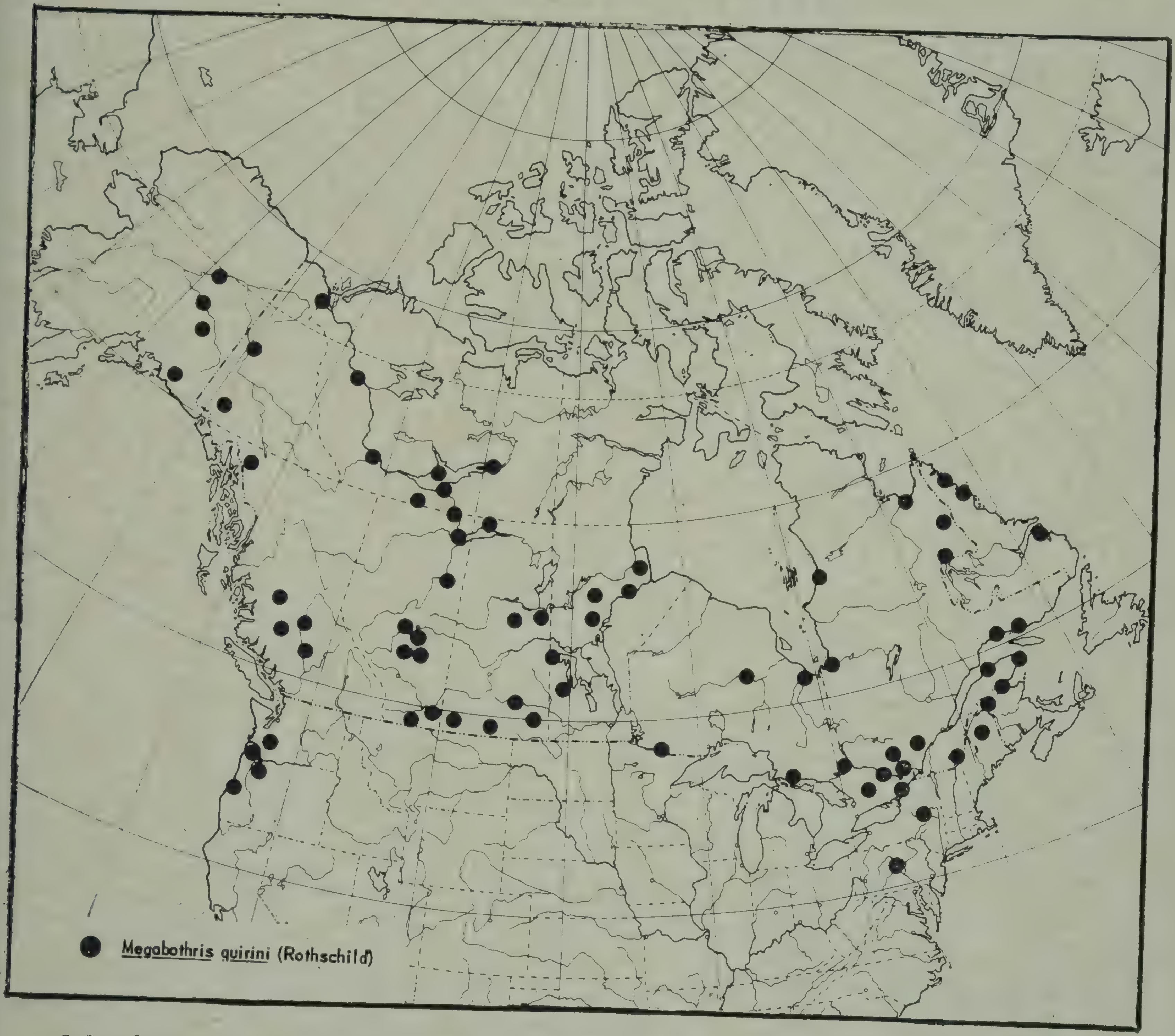
Opisodasys pseudarctomys (Baker) on flying squirrels, *Glaucomys sabrinus* ssp.;

Opisocrostis tuberculatus (Baker) on ground squirrels, *Citellus* spp.

The 19 species listed are rather widely distributed across the Canadian Zone of the Continent, some of them extending northward well into the Hudsonian, and others southward into the northern parts of the Austral Region. A few are "western" rather than transcontinental, but virtually none has penetrated west of the Coast Mountains. Fourteen of the species represent genera (seven) that are known also from Asia, although in most, though not all, instances the species are not especially close. The remaining four genera (five species) are strictly Nearctic. It seems most likely that all of this group of species originated from areas lying to the south of the major ice sheets.

Of this group, the distributions of *Peromyscopsylla hamifer*, *Megabothris asio*, and *Monopsyllus thambus*, have already been discussed.

The widely distributed, though scarce in collections, *Rhadinopsylla fraterna* is of special interest as it is now believed to be represented in the Palaearctic region by a number of subspecies of which one occurs as far away as Swedish Lapland.



Megabothris quirini, which occurs on many species of mice, and which seems to be the only regular flea of the jumping mice *Zapus* and *Napaeozapus* has an extremely broad distribution (Fig. 6), corresponding roughly to that of the family Zapodidae. It borders the Arctic Zone from central Alaska to northern Labrador, and extends from western Oregon to the northern Atlantic States. In British Columbia, it does not appear to occur west of the Coast Range. It is related to the lemming flea, *M. groenlandicus*, to which it is almost allopatric.

Corrodopsylla curvata curvata, on several species of shrews, has a similar distribution, and again, does not reach the Pacific Coast.

One or two northern records of the ground squirrel fleas, *Oropsylla rupestris* and *Opisocrostis tuberculatus*, are available, and caused some surprise as the fleas are otherwise not known from the northern *Citellus undulatus*, but occur commonly farther south in the Transition Zone on the common prairie "gopher" *Citellus richardsoni* Sabine. Their distributions must be widely disrupted, for many hundreds of miles intervene between the ranges of the northern and southern ground squirrels, and the fleas are not regularly found on any other hosts. I have not yet been able to detect any subspecific differences.

Megabothris atrox a flea of mink and weasels, *Mustela* spp., is known from only a few records, but appears to be broadly distributed in the Canadian and Hudsonian zones of central Canada.

EASTERN SPECIES

Nearctopsylla genalis genalis (Baker) on moles and shrews;

Peromyscopsylla catatina (Jordan) on Microtinae.

One or two records from northern Quebec are available for these typically eastern North American species. Their presence in the north undoubtedly represents post-glacial invasion.

CONCLUSION

The foregoing account of flea distribution in the north must be considered provisional to a considerable extent. Fleas are difficult to collect satisfactorily, and many of the species are active as adults principally during the winter months when collectors are seldom active, or at least not active in the right localities. Therefore, the apparent absence of some of the species from certain areas should not be regarded too seriously at this time. Then again, decisions on the precise relationships between many Nearctic and Palaearctic forms must await an actual comparison of specimens. Finally, the all-important relationships between Palaearctic and Nearctic mammals require further critical study and elucidation. However, I suggest that clear indications of close affinities between certain fleas (especially those that tend to be host-specific) of the Old and New Worlds and within the New World, might be weighed by the mammalogists, along with other evidence, in assisting them to arrive at their final taxonomic and zoogeographic conclusions.

REFERENCES

Burt, W. H., and R. P. Grossenheider. 1952. A field guide to the mammals. *Houghton Mifflin Company*, Boston. 200 pp.

Cameron, A. W. 1952. Notes on mammals of Yukon. *Nat. Mus. Can. Bull.* 126: 176–187.

Deevey, E. S., Jr. 1949. Biogeography of the Pleistocene. *Bull. Geol. Soc. Amer.* 60: 1315–1416.

Flint, R. F. 1952. The ice age in the North American Arctic. *Arctic* 5: 135–152.

Hibbard, C. W. 1949. Pleistocene vertebrate palaeontology in North America. *Bull. Geol. Soc. Amer.* 60: 1417–1428.

Holland, G. P. 1949. The Siphonaptera of Canada. *Canada Dept. Agr. Tech. Bull.* 70: 306 pp.

Holland, G. P. 1950a. Notes on some British Columbian fleas, with remarks on their relationships and distribution. *Proc. Ent. Soc. B.C.* 46: 5–13.

Holland, G. P. 1950b. Notes on *Megabothris asio* (Baker) and *M. calcarifer* (Wagner) with the description of a new subspecies (Siphonaptera: Ceratophyllidae). *Canadian Ent.* 82: 126–133.

Holland, G. P. 1952. Descriptions of fleas from northern Canada. *Canadian Ent.* 84: 297–308.

Hopkins, G. H. E., and M. R. Rothschild. 1956. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum. Vol. 2: 445 pp.

Hubbard, C. A. 1947. Fleas of western North America. *Iowa State College Press*, Ames. 533 pp.

Ioff, I. G., and O. I. Scalon. 1954. Handbook for the identification of the fleas of eastern Siberia, the far east, and adjacent regions [In Russian]. *State publishing house of Medical literature*, Medgiz, Moscow. 275 pp.

Jellison, W. L., and G. M. Kohls. 1939. Siphonaptera: a list of Alaskan fleas. *Pub. Hlth. Repts.* 51: 842–844.

Munro, J. A., and I. McT. Cowan. 1947. A review of the bird fauna of British Columbia. *B.C. Prov. Mus. Special Pub.* 2: 285 pp.

Rand, A. L. 1954. The ice age and mammal speciation. *Arctic* 7: 31–35.

Rausch, R. 1950. Notes on microtine rodents from the Brooks Range, Arctic Alaska. *J. Wash. Acad. Sci.* 40: 133–136.

Rausch, R. 1953. On the status of some Arctic mammals. *Arctic* 6: 91–148.

Simpson, G. G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. *Bull. Geol. Soc. Amer.* 58: 613–687.

Smit, F. G. A. M. 1953. The presence in Scotland of *Tarxopsylla octodecimdentata* (Kol.) a flea hitherto unrecorded from the British Isles. *Scot. Nat.* 65: 5–10.

Wagner, J. 1936. The fleas of British Columbia. *Canadian Ent.* 68: 193–207.

The Distribution of Arctic and Subarctic Butterflies[1]

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ABSTRACT

The paper deals with the distributional patterns of 26 species of butterflies indigenous to the Arctic and the Subarctic (Hudsonian) regions of Northern Canada. These patterns are divided into major types and are correlated wherever possible with biological and physical factors. The distributions suggest three main refugia for these butterflies during the Pleistocene period.

This study was based mainly on the collections made by (1) the Canadian Northern. Insect Survey, (2) the Canadian Arctic Expedition 1913–1918, (3) various members of the Geological Survey of Canada and other officers of Canadian Government Departments. The area under consideration is mainly that part of arctic and subarctic Canada that extends east of the Rocky Mountains or Cordilleran region, and particularly the area east of the MacKenzie River.

The localities investigated by the Canadian Northern Insect Survey are marked by a dot on each map. (See caption to Fig. 1 for reference to place names.) The known distributional records are shown by a circle or a triangle. The maps also contain an outline of the northern limit of coniferous tree growth, and in general, the extent of the Northern Transition or Hudsonian Zone adjacent to it. This latter zone is an admixture of biological and physical components of the arctic or treeless area to the north, and the coniferous forest or Canadian Zone to the south. It is usually referred to as the subarctic region. The northern boundary of this region approximates the northern limit of tree growth. The southern boundary is more cryptic and interwoven into the environmental complexities of the coniferous forest or of the tree-less alpine or maritime regions. The distributional patterns that are shown do not necessarily represent the total distribution of the species. Many of them extend into higher elevations within the Cordilleran System, some extend into Alaska, and some are holarctic.

In this discussion, I do not deal with geographical variation within the distributional limits of the species, but will present the distributional patterns, attempt to correlate these patterns with some biological or physical factors, and suggest the apparent regions of refugia during the Pleistocene glacial period. I shall mention, however, that geographical subspeciation and clinal tendencies occur frequently and are complex. The geographical variation within the range of the species follows the distributional patterns east and west, and north and south. As an example, there is a great tendency for the northern butterfly species to become darker and more hairy in the northern portion of their range. This is probably an adaptation that enables the adult butterflies to trap the heat from solar radiation, and allows them to be active when the sun is shining, even though the air temperature is too low for normal activity.

You will notice that many of the localities where the various arctic species have been taken are coastal ones. This in no way implies that the species have a coastal distribution, but merely represents localities where collecting was done. The lack of transportation, except by water for many years, necessitated the establishment of settlements adjacent to the sea, or on navigable rivers.

Figs. 2–17 show the known Canadian distribution of 16 species or subspecies of butterflies that only exist in the treeless arctic or occasionally in arctic environments in the transition region to the south. The map sequence shows a gradual range extension from west to east. Note that the range of some of the species such as *Erebia fasciata* Butl. (Fig. 4) stops at the west coast of Hudson Bay. Others extend north and east in successive stages through the islands of the Arctic Archipelago to northern Quebec (Figs. 5–17). This suggests a post glacial entry route from the north-west.

The distribution of *Lycaena phlaeas feildeni* McLach. (Fig. 6) suggests that there may have been two Pleistocene refugia for this butterfly, one in the arctic Archipelago and one in the northern Cordilleran region. The few specimens I have seen from the latter region appear subspecifically distinct from those inhabiting the central arctic and arctic islands. I doubt very much if the above specimens are conspecific with *L. phlaeas americana* Harr., a form that occurs far to the south. The two are separated by great gaps in distance and/or in environment.

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Erebia youngi Holl. (Fig. 2) is an Alaskan species that enters Canada only near the Alaskan border in the Yukon.

The distribution of *Boloria pales* D. and S. (Fig. 3) may be correlated with the Precambrian sedimentary formation from near the Mackenzie delta, southeast to Baker Lake, N.W.T. In the latter vicinity, the sediments are abruptly displaced on the surface by Precambrian granites and the distribution of this species, as far as is known, also abruptly terminates. The apparent restricted distribution of *Colias pelidne* Bdv. (Fig. 14) in southern Baffin Island, northern Quebec, and in arctic alpine areas in southern British Columbia and Alberta is unique among the northern butterflies. On a distributional interpretation, *C. pelidne* is the eastern arctic counterpart of the western arctic *C. palaeno chippewa* Kby. (Fig. 13). It is quite probable that *pelidne* and *chippewa* are subspecies of a single species and specifically distinct from the European *palaeno* L.

The origin and specificity of *Colias boothii* Curt. has been a subject of taxonomic speculation for many years. However, this species is readily recognized in series, and has a normal arctic distribution from the barrens of Alaska, east to Southampton and northern Baffin Islands (Fig. 5). The closely allied species *C. nastes* Bdv. (Fig. 11) and *C. hecla* Lef. (Fig. 10) extend farther east, and south to the treeless regions of northern Quebec, where *boothii* has never been taken.

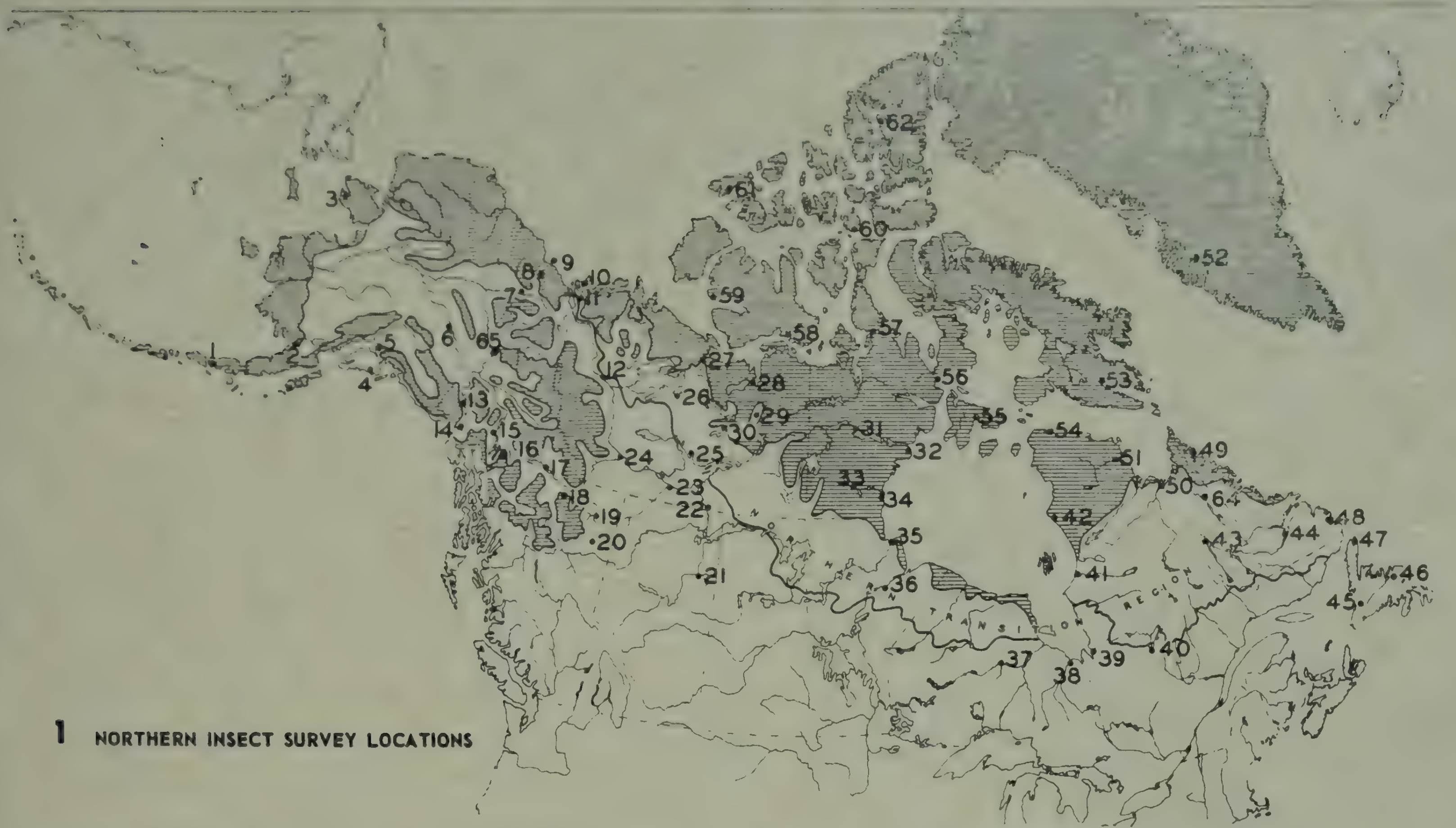
Oeneis taygete Geyer (Fig. 15), *O melissa* Fabr. (Fig. 16) and *O. polixenes* Fabr. (Fig. 17) are arctic species that occur as relict populations at elevations above tree-line in the Gaspé region of Quebec. *O. melissa* also occurs in a similar environment in New Hampshire, and *O. polixenes* in Maine.

Figs. 18–21 represent the known Canadian distribution of *Boloria frigga* Thun, *B. freija* Thun., *B. eunomia* Esp., and *Plebeius aquilo* Bdv. These show geographical variation from the arctic to the northern coniferous zone. These northern and southern populations are currently listed as subspecies. It is quite probable that further studies will reveal that some of the supposed subspecies may be specifically distinct.

The absence of *Boloria eunomia s. lat.* (Fig. 20) from Coral Harbor, Chesterfield, Repulse Bay, and the Arctic Archipelago, and its presence in the Arctic region of northern Quebec and Labrador suggest a post glacial entry from the south. *Boloria frigga s. lat.* (Fig. 18) has not been collected from Chesterfield, Coral Harbor or the arctic regions of northern Quebec and Labrador. However, it does occur across the southern part of the Arctic Archipelago to Frobisher Bay in southern Baffin Island. This distribution suggests a post glacial entry route from the northwest in a bilineal manner, one arm going north and one south of Hudson Bay, neither of which has extended to the Arctic region from Chesterfield through Southampton Island and arctic Quebec and Labrador.

Fig. 1. Localities of the Canadian Northern Survey: 1, Cold Bay, Alaska; 2, Naknek, Alaska; 3, Nome, Alaska; 4, Seward, Alaska; 5, Anchorage, Alaska; 6, Big Delta, Alaska; 7, Rampart House, Yukon; 8, Firth River, Yukon; 9, Herschel Island, Yukon; 10, Kidluit Bay, N.W.T.; 11, Reindeer Depot, N.W.T.; 12, Norman Wells, N.W.T.; 13, Burwash Landing, Yukon; 14, Haines Cut-Off, Yukon; 15, Whitehorse, Yukon; 16, Atlin Lake, B.C.; 17, Watson Lake, Yukon; 18, Muncho Lake, B.C.; 19, Fort Nelson, B.C.; 20, Mason Creek, B.C.; (13–15, 17–20, Alaska Highway Expedition); 21, Fort McMurray, Alta.; 22, Fort Smith, N.W.T.; 23, Hay River, N.W.T.; 24, Fort Simpson, N.W.T.; 25, Yellowknife, N.W.T.; 26, Saw Mill Bay, N.W.T.; 27, Coppermine, N.W.T.; 28, Bathurst Inlet, N.W.T.; 29, Muskox Lake, N.W.T.; 30, MacKay Lake, N.W.T.; 31, Baker Lake, N.W.T.; 32, Chesterfield, N.W.T.; 33, Padlei, N.W.T.; 34, Eskimo Point, N.W.T.; 35, Churchill, Man.; 36, Gillman, Man.; 37, Ogoki Post, Ont.; 38, Moosonee, Ont.; 39, Rupert House, Que.; 40, Mistassini Post, Que. ;41, Great Whale River, Que.; 42, Port Harrison, Que.; 43, Knob Lake, Que.; 44, Goose Bay, Nfld.; 45, Harmon Field, Nfld.; 46, Gander, Nfld.; 47, St. Anthony, Nfld.; 48, Cartwright, Nfld.; 49, Hebron, Nfld.; 50, Fort Chimo, Que.; 51, Payne Bay, Que.; 52, Sondrestrom Fiord, Greenland; 53, Frobisher Bay, N.W.T.; 54, Sugluk, Que.; 55, Coral Harbor, N.W.T.; 56, Repulse Bay, N.W.T.; 57, Spence Bay, N.W.T.; 58, Cambridge Bay, N.W.T.; 59, Holman Island, N.W.T.; 60, Resolute Bay, N.W.T.; 61, Mould Bay, N.W.T.; 62, Eureka, N.W.T.; 63, Alert, N.W.T.; 64, Indian House Lake, Que.

Figs. 2–27. Distribution of northern butterflies.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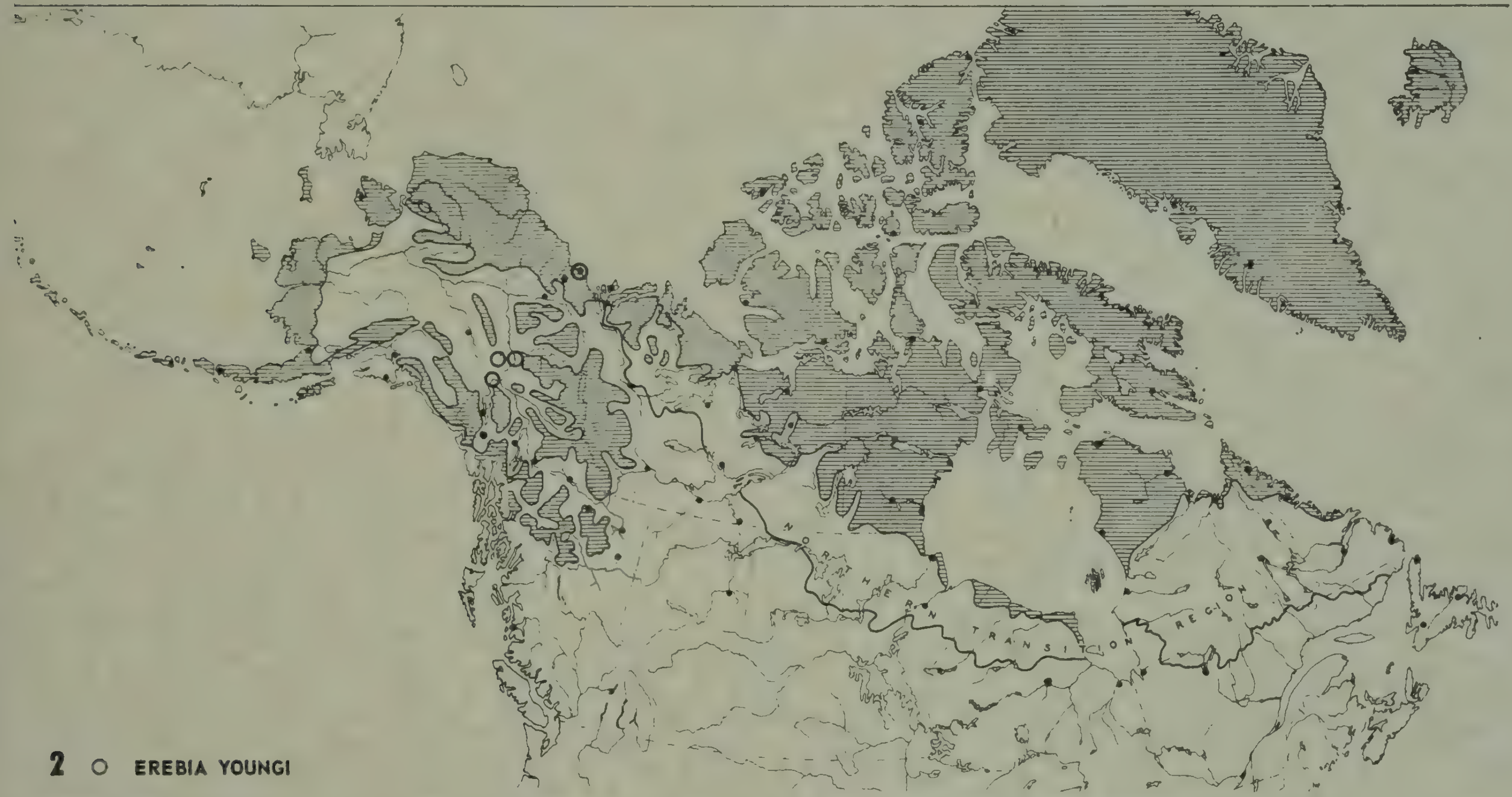
NORTHERN TRANSITION REGION

1 NORTHERN INSECT SURVEY LOCATIONS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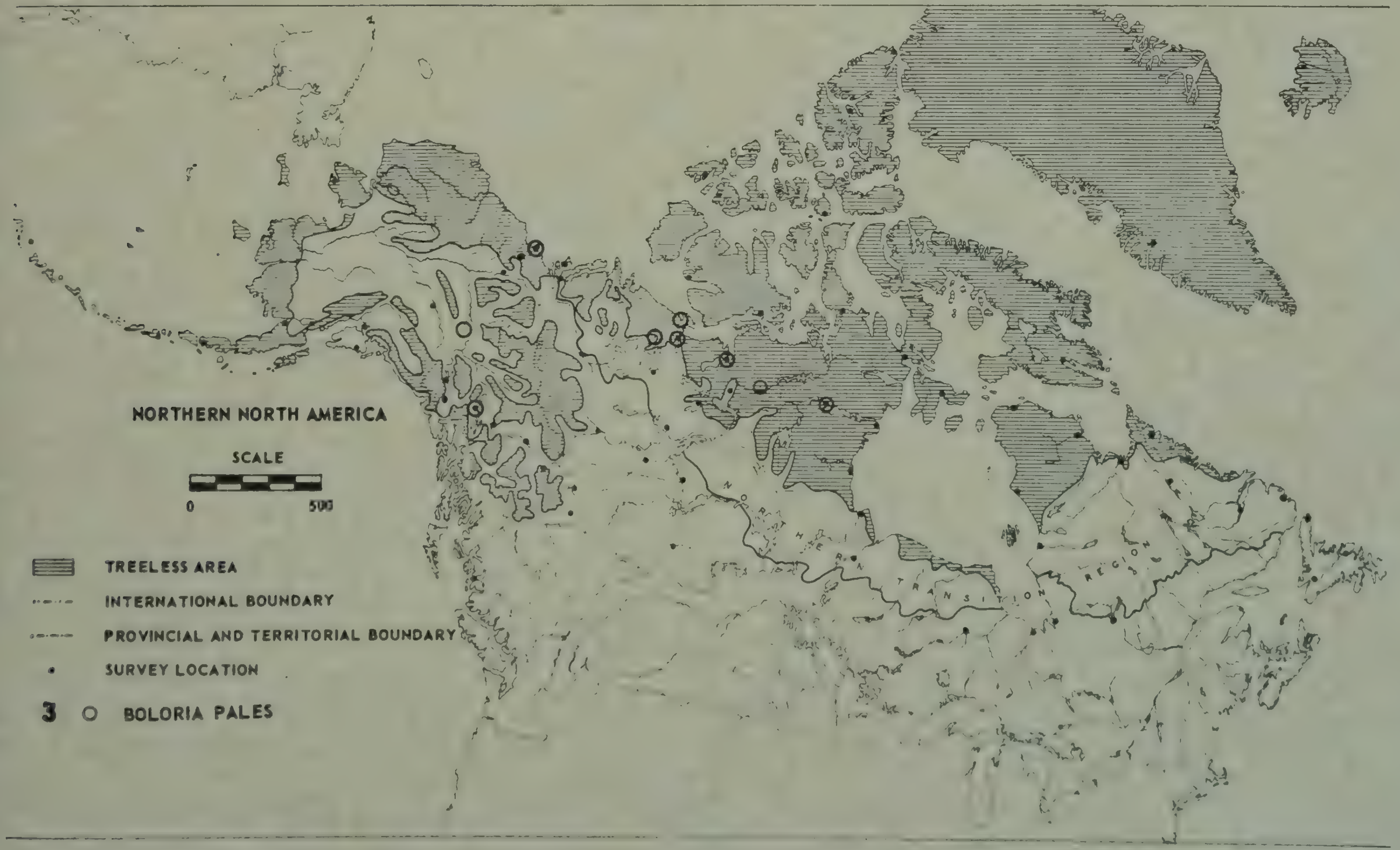
2 ○ EREBIA YOUNGI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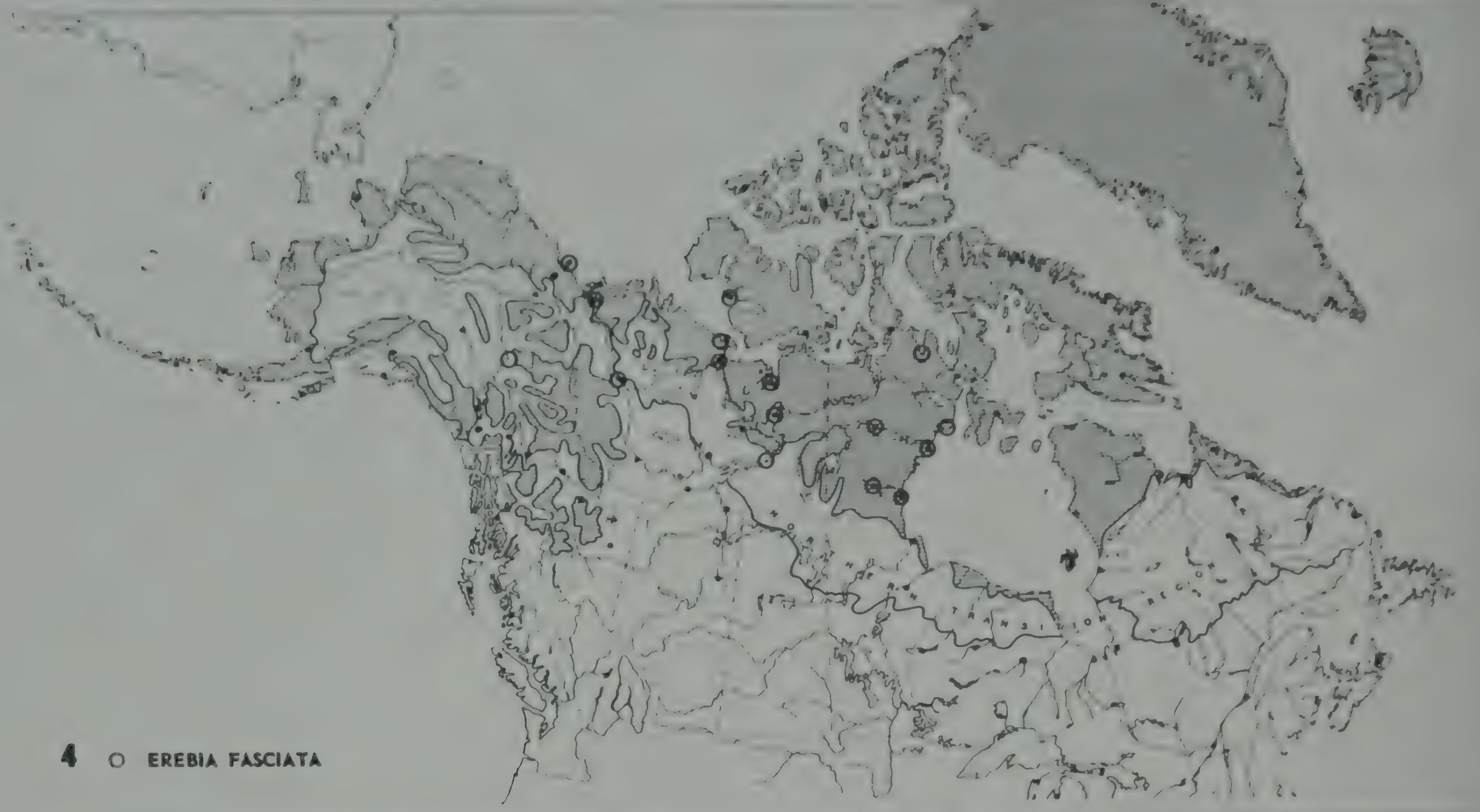
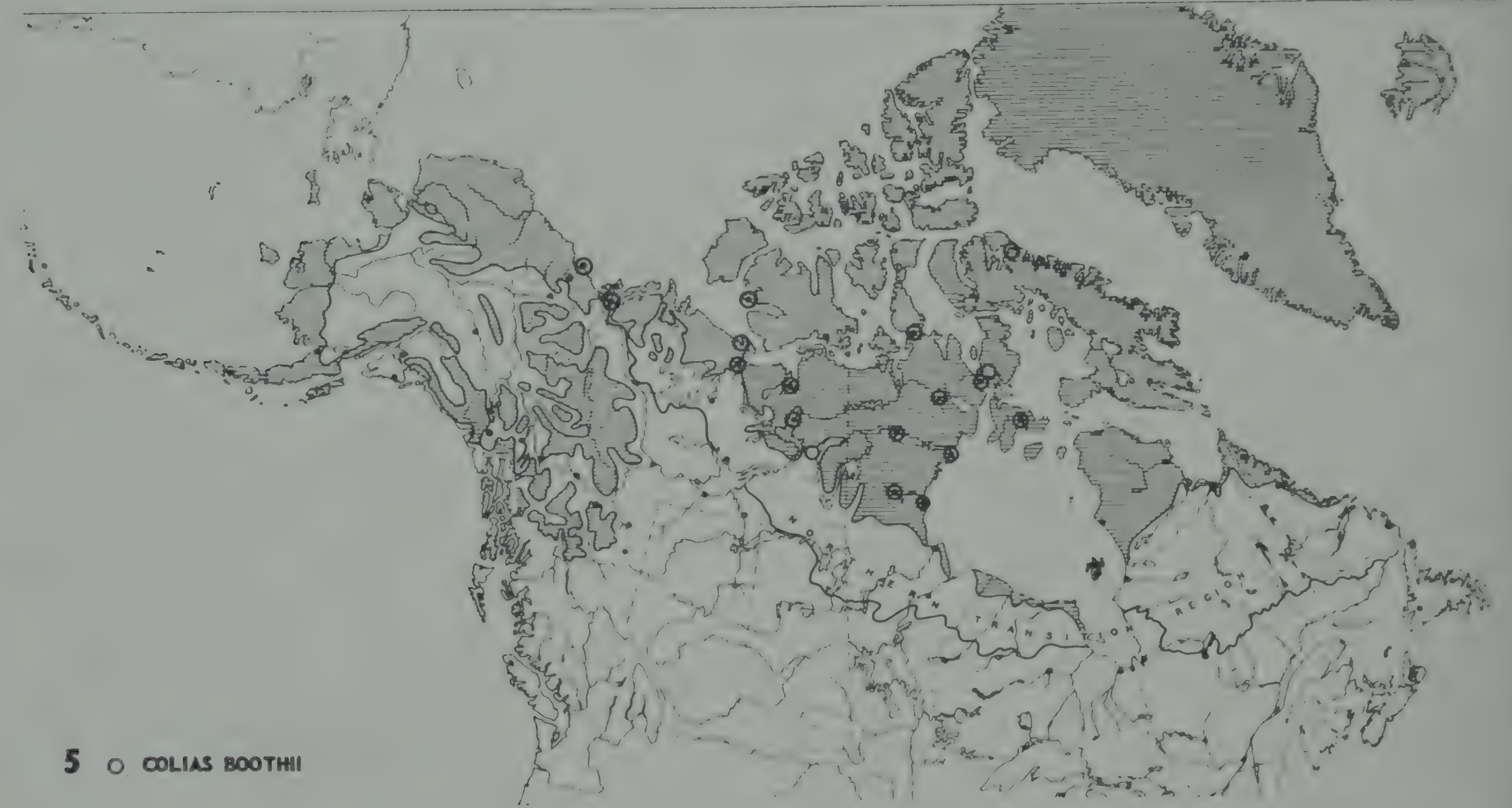
NORTHERN TRANSITION REGION

3 ○ BOLORIA PALES


TRANSITION
REGION

4 ○ EREBIA FASCIATA


TRANSITION
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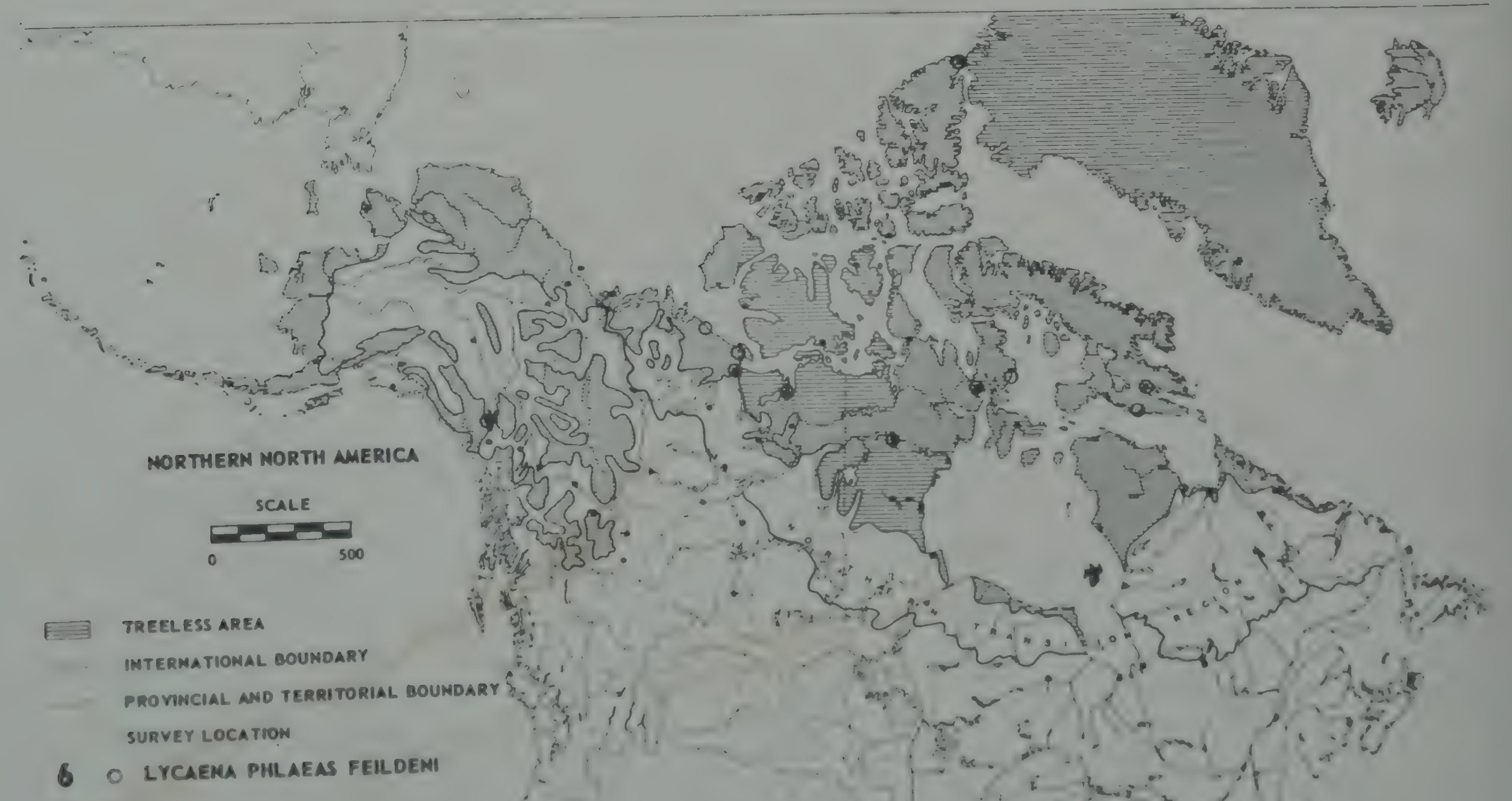
5 ○ COLIAS BOOTHII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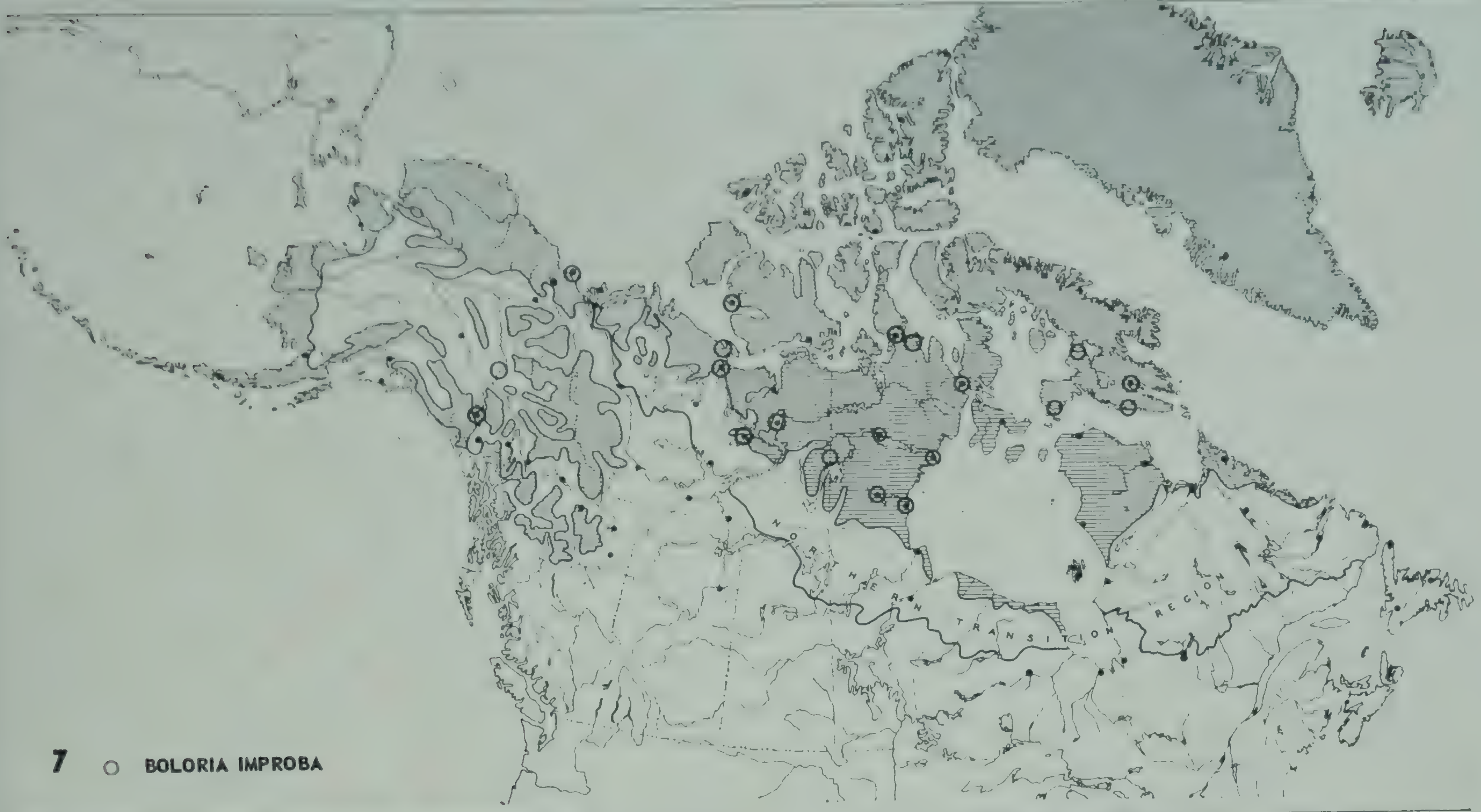
6 ○ LYCAENA PHLAEAS FEILDENI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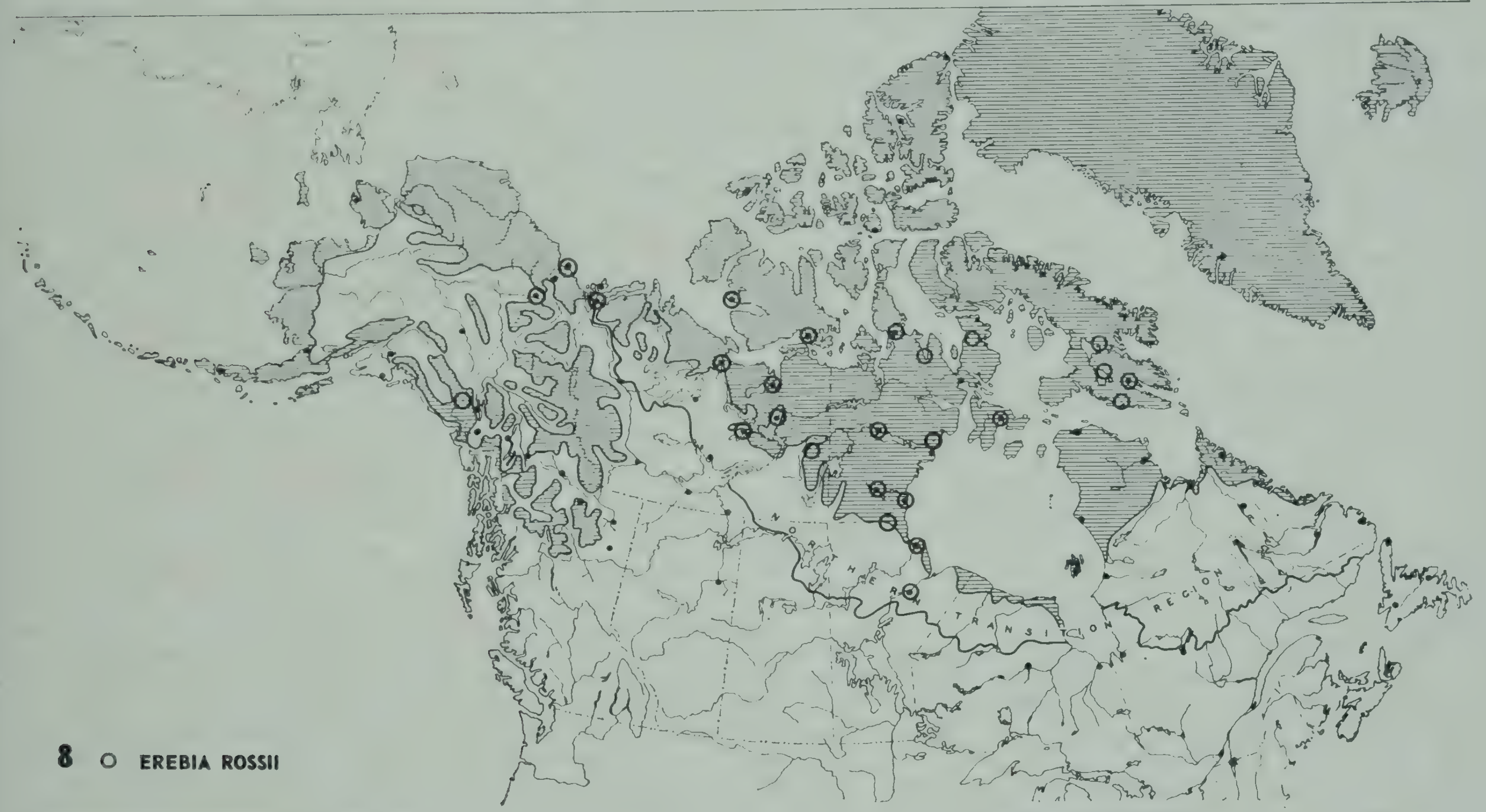
7 ○ BOLORIA IMPROBA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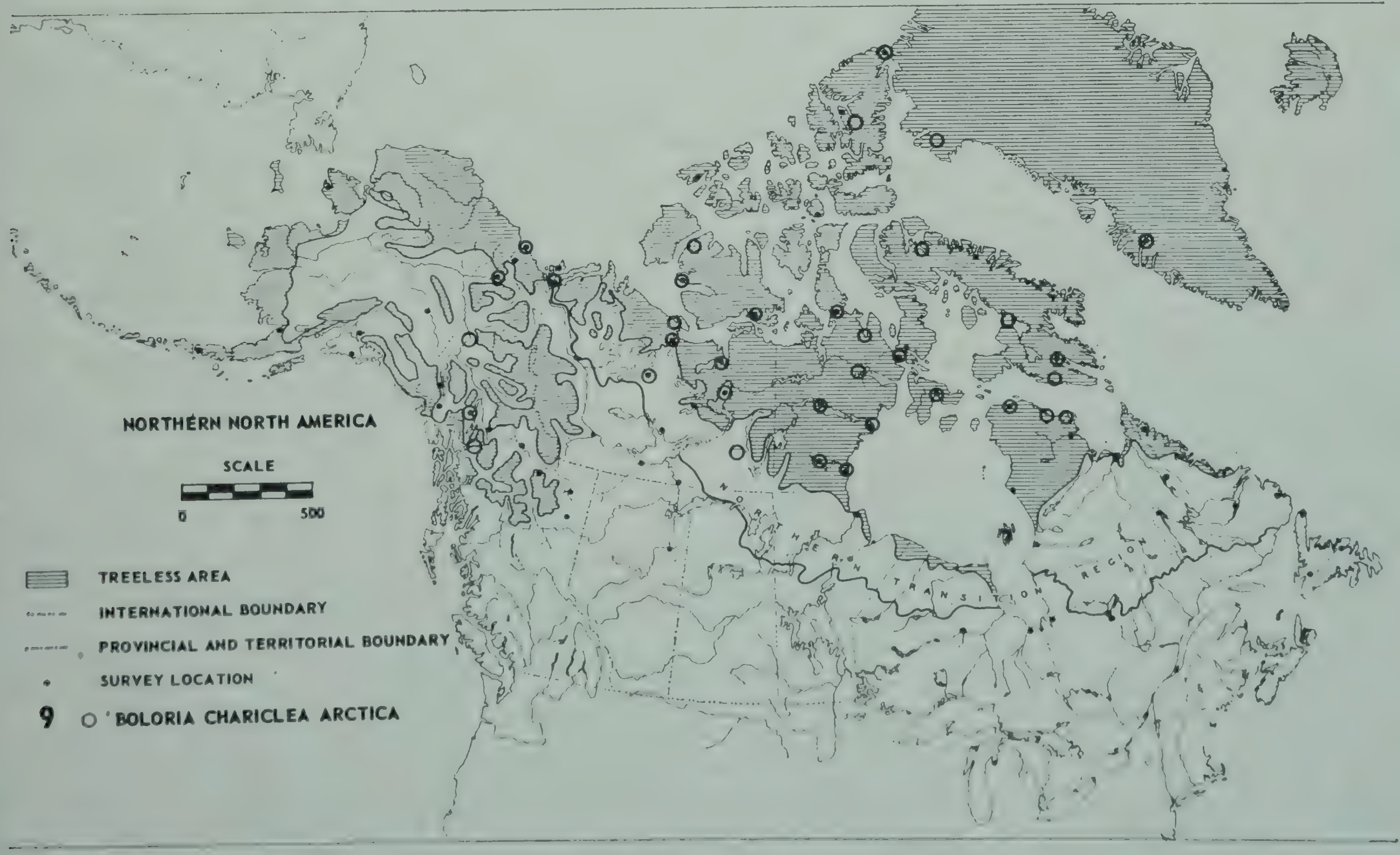
8 ○ EREBIA ROSSII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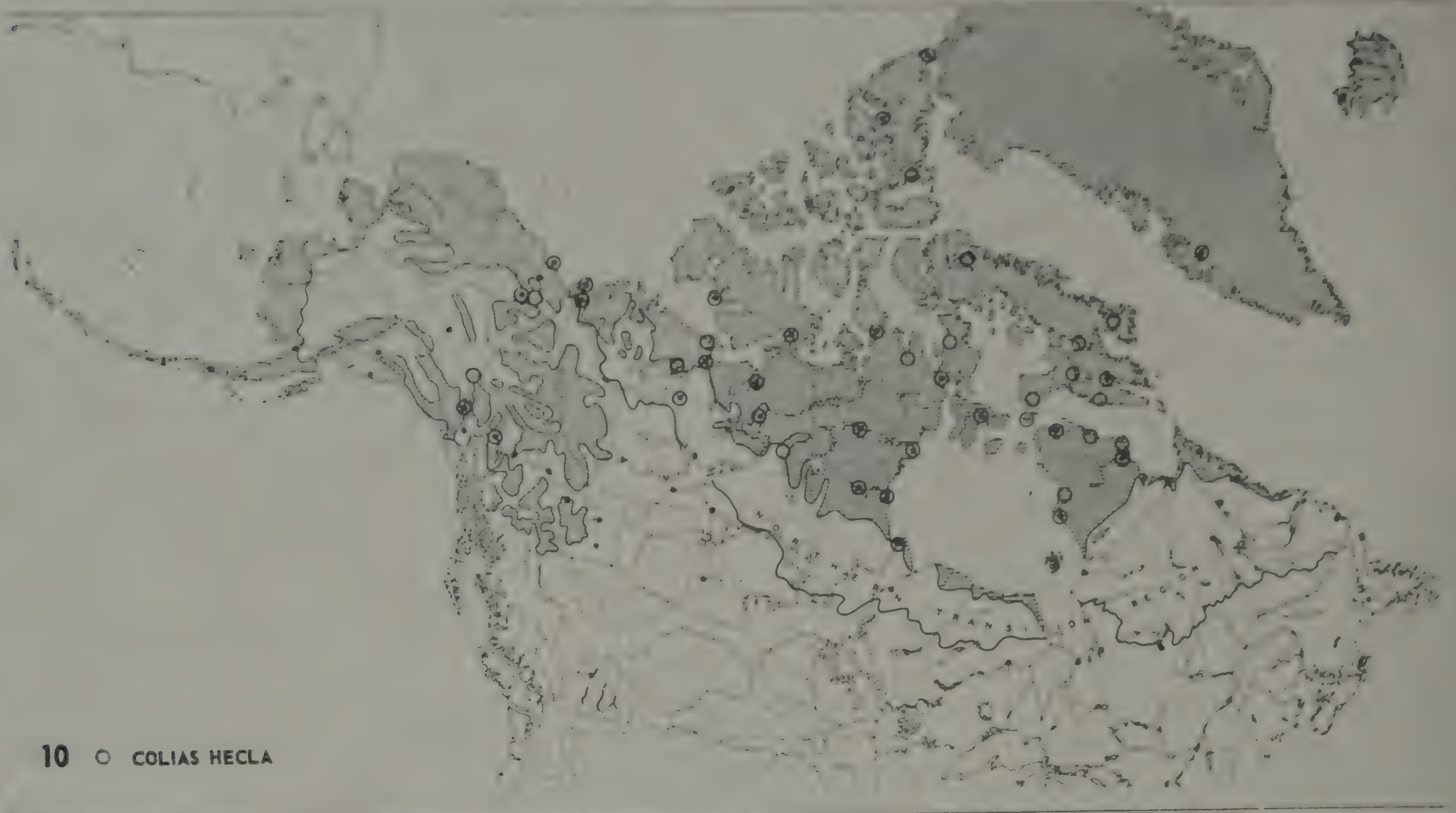
9 ○ BOLORIA CHARICLEA ARCTICA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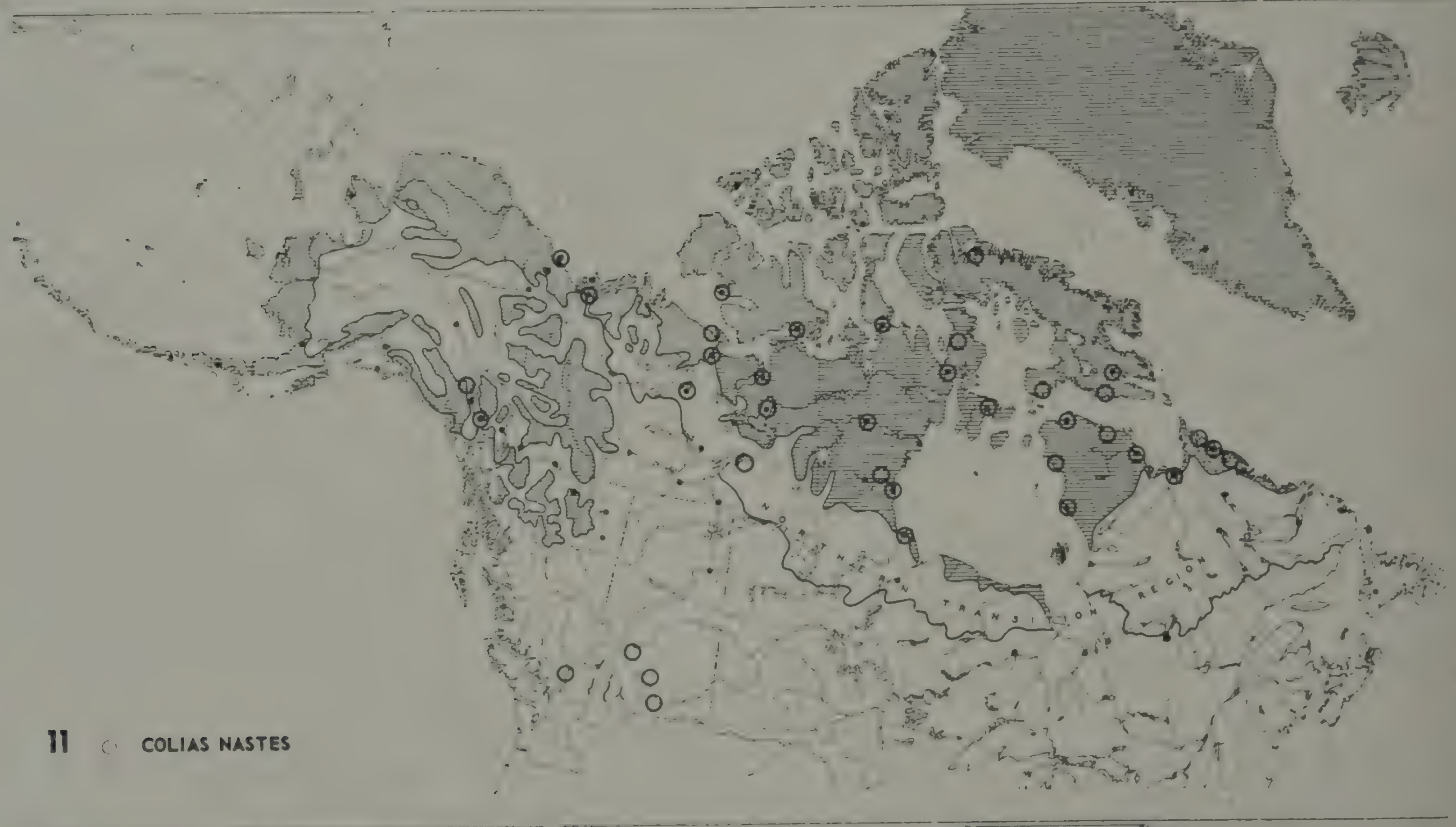
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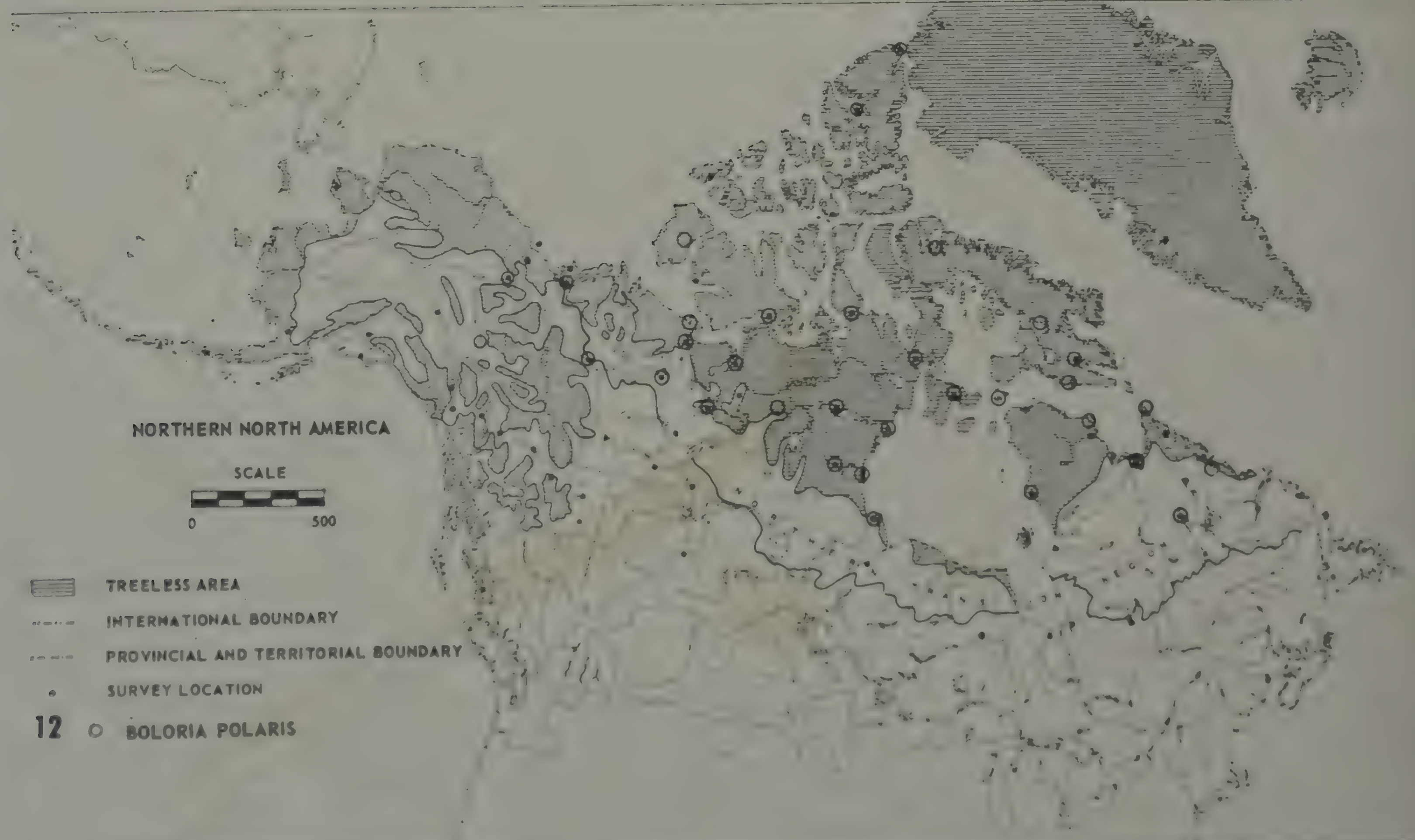
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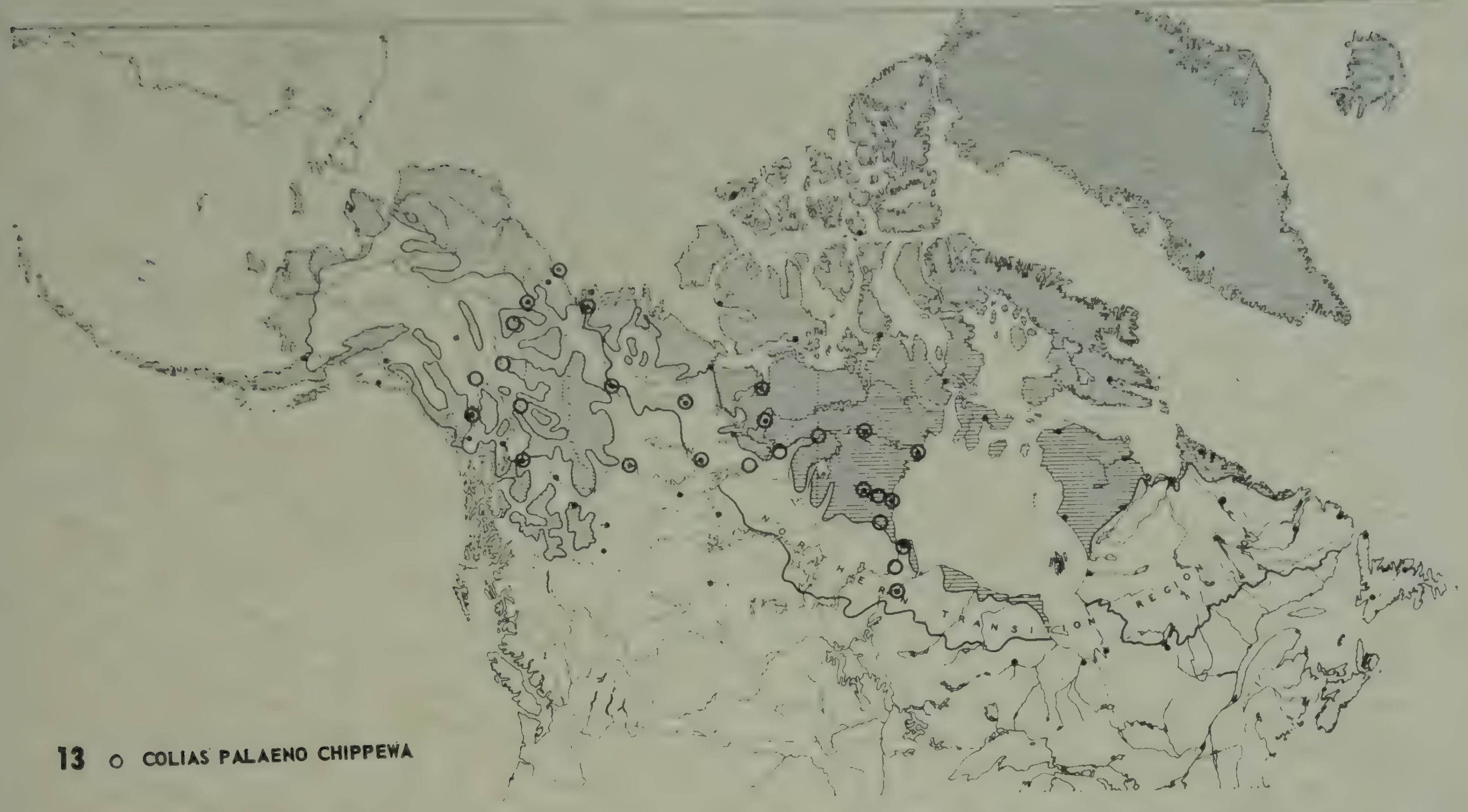
12 ○ BOLORIA POLARIS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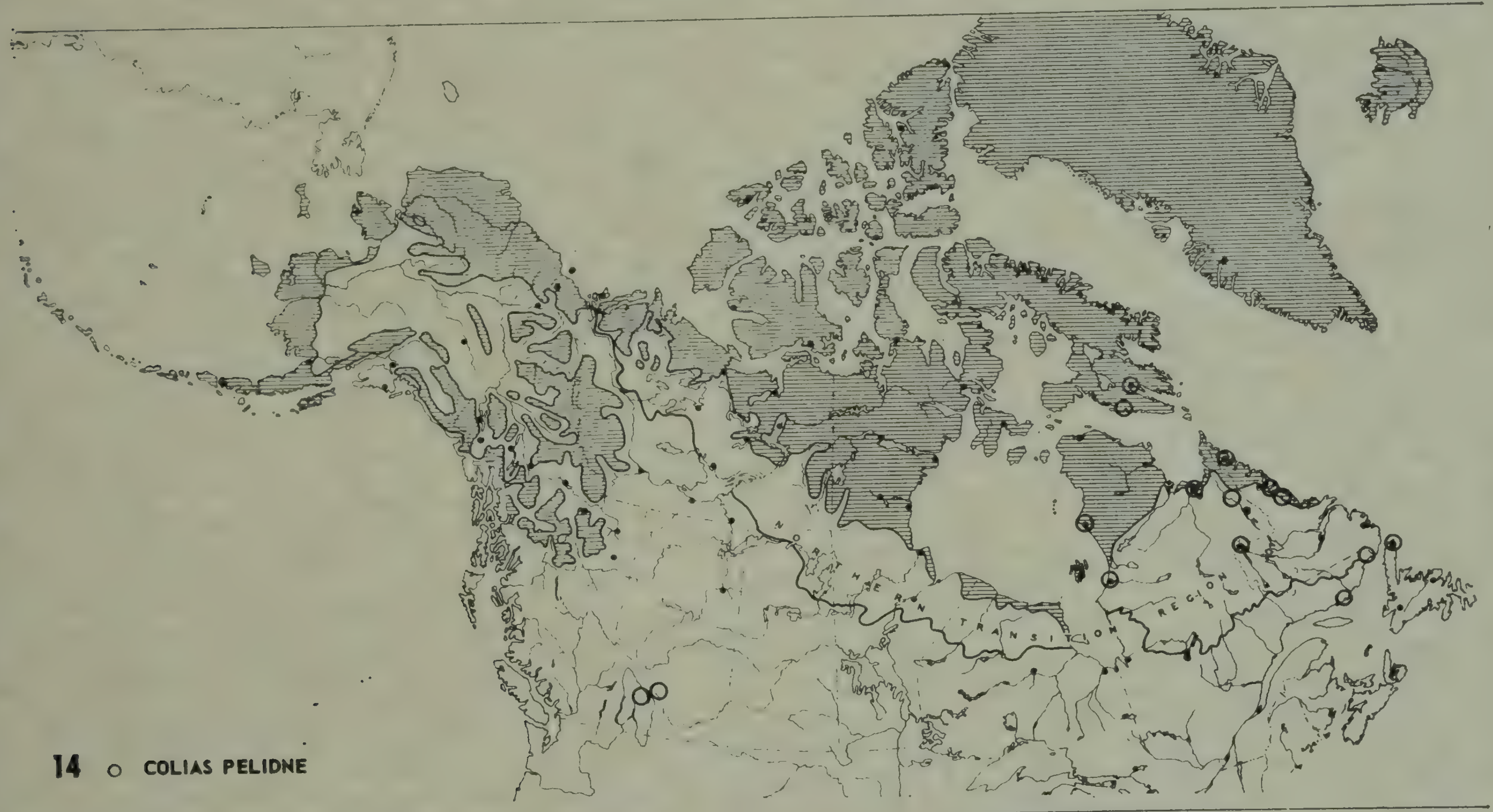
13 ○ COLIAS PALAENO CHIPPEWA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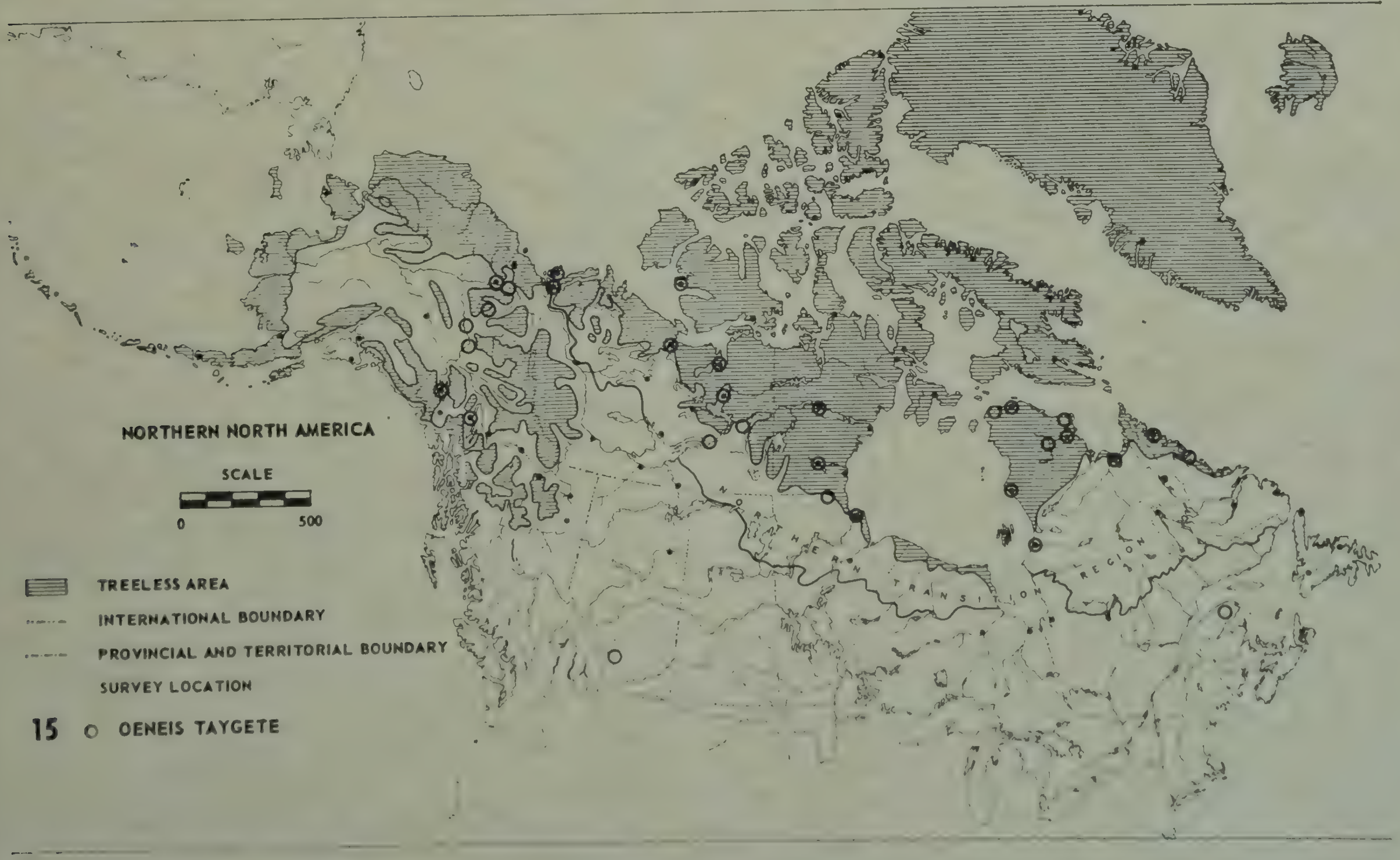
14 ○ COLIAS PELIDNE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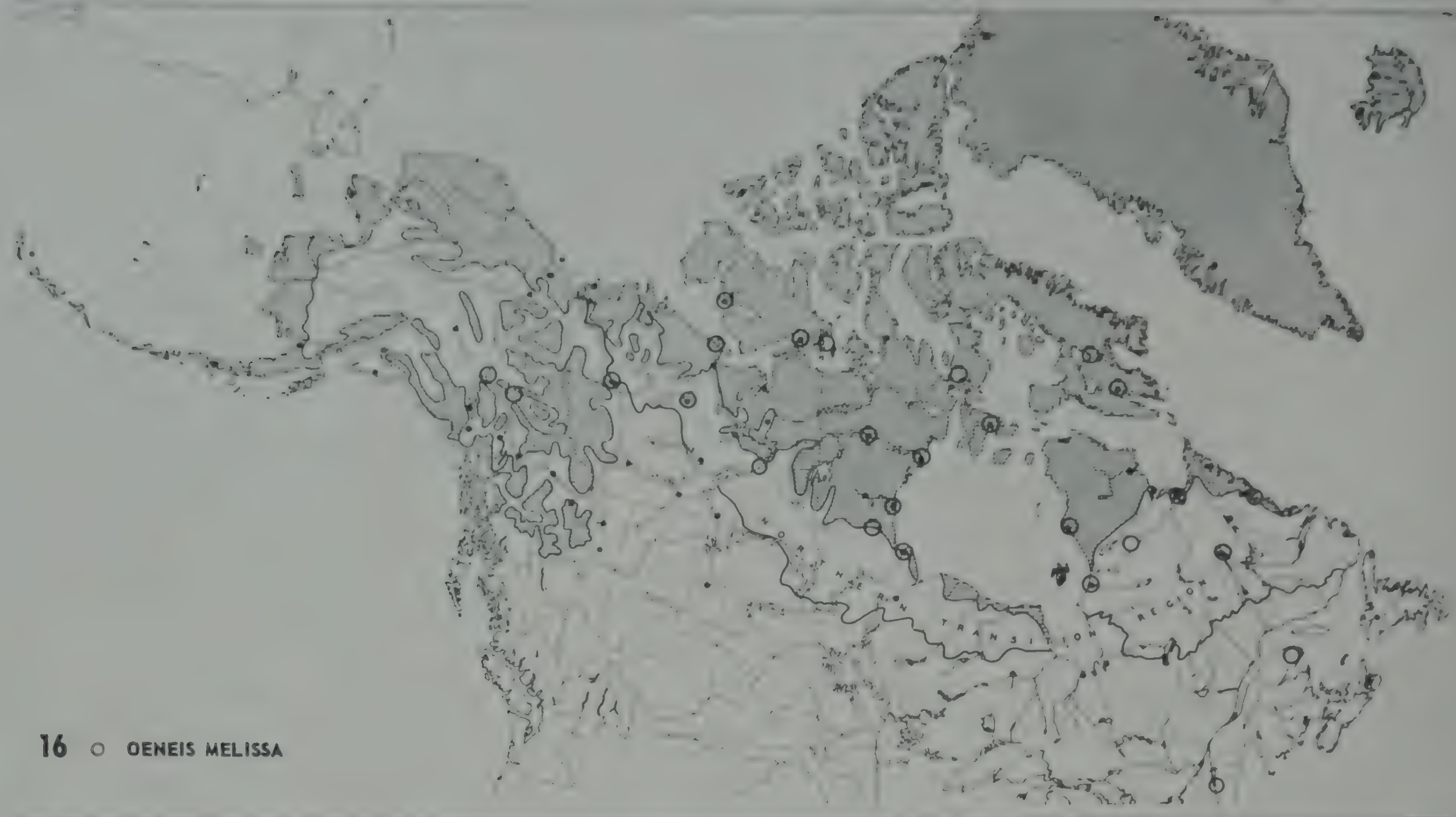
NORTHERN TRANSITION REGION

15 ○ OENEIS TAYGETE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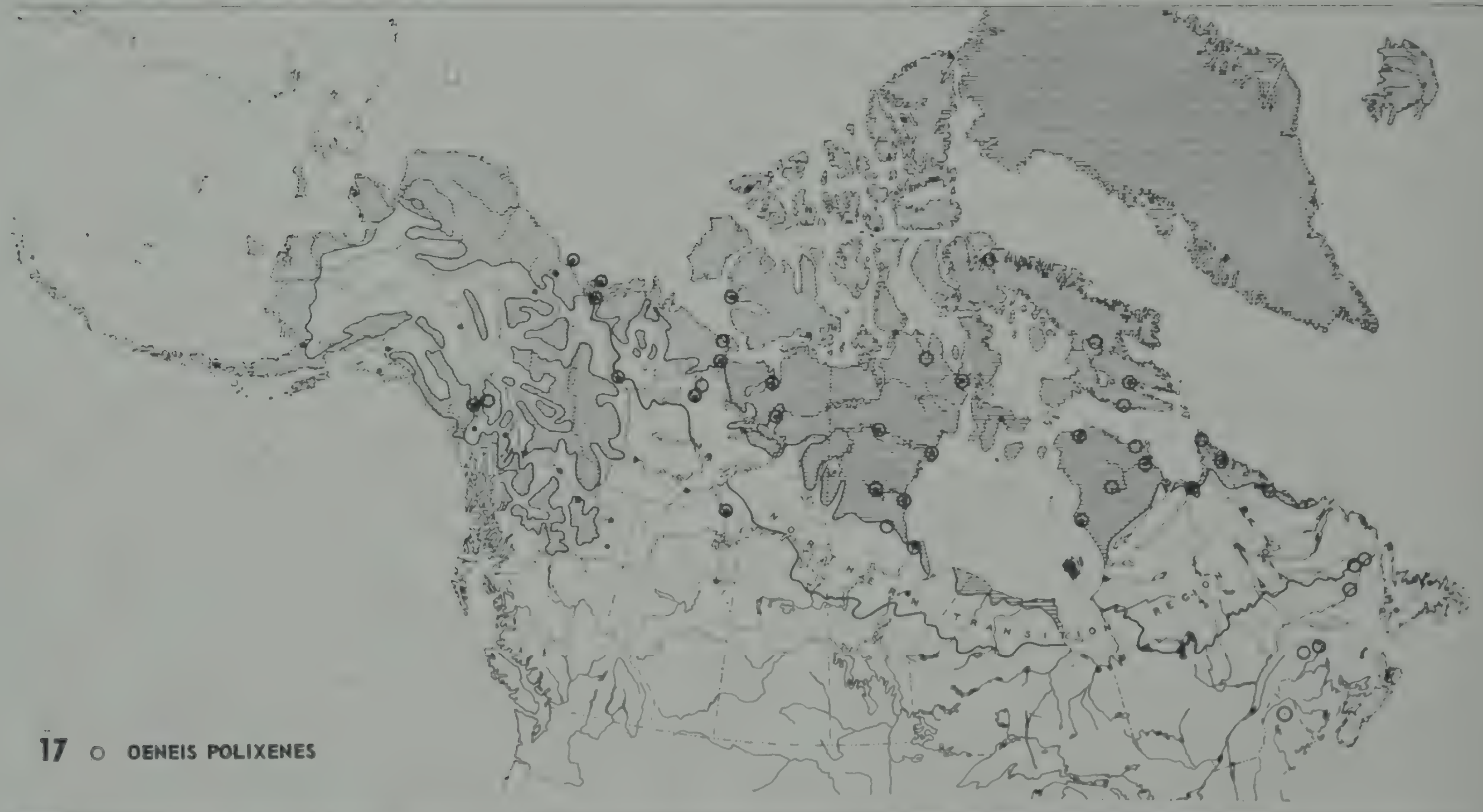
16 ○ OENEIS MELISSA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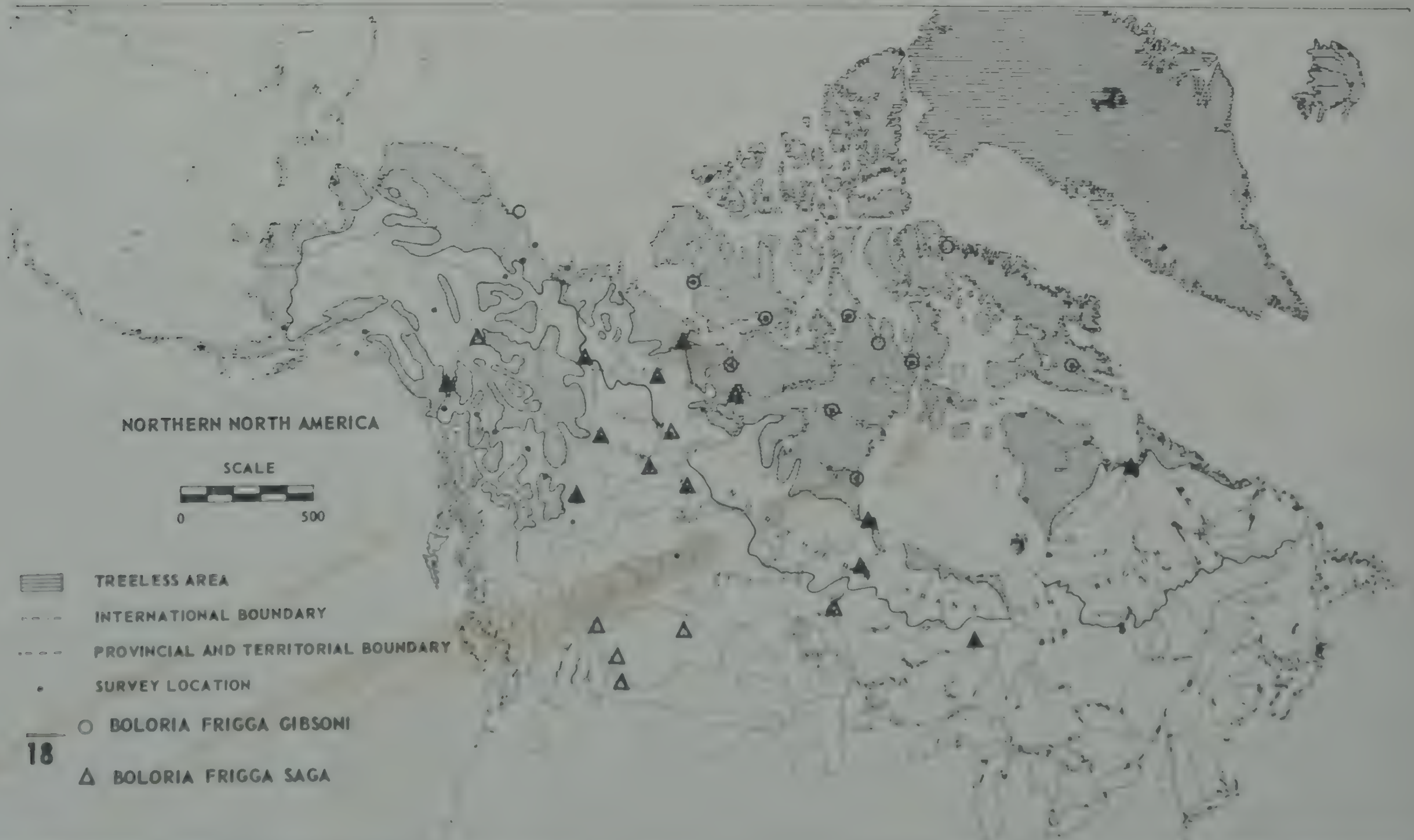
17 ○ OENEIS POLIXENES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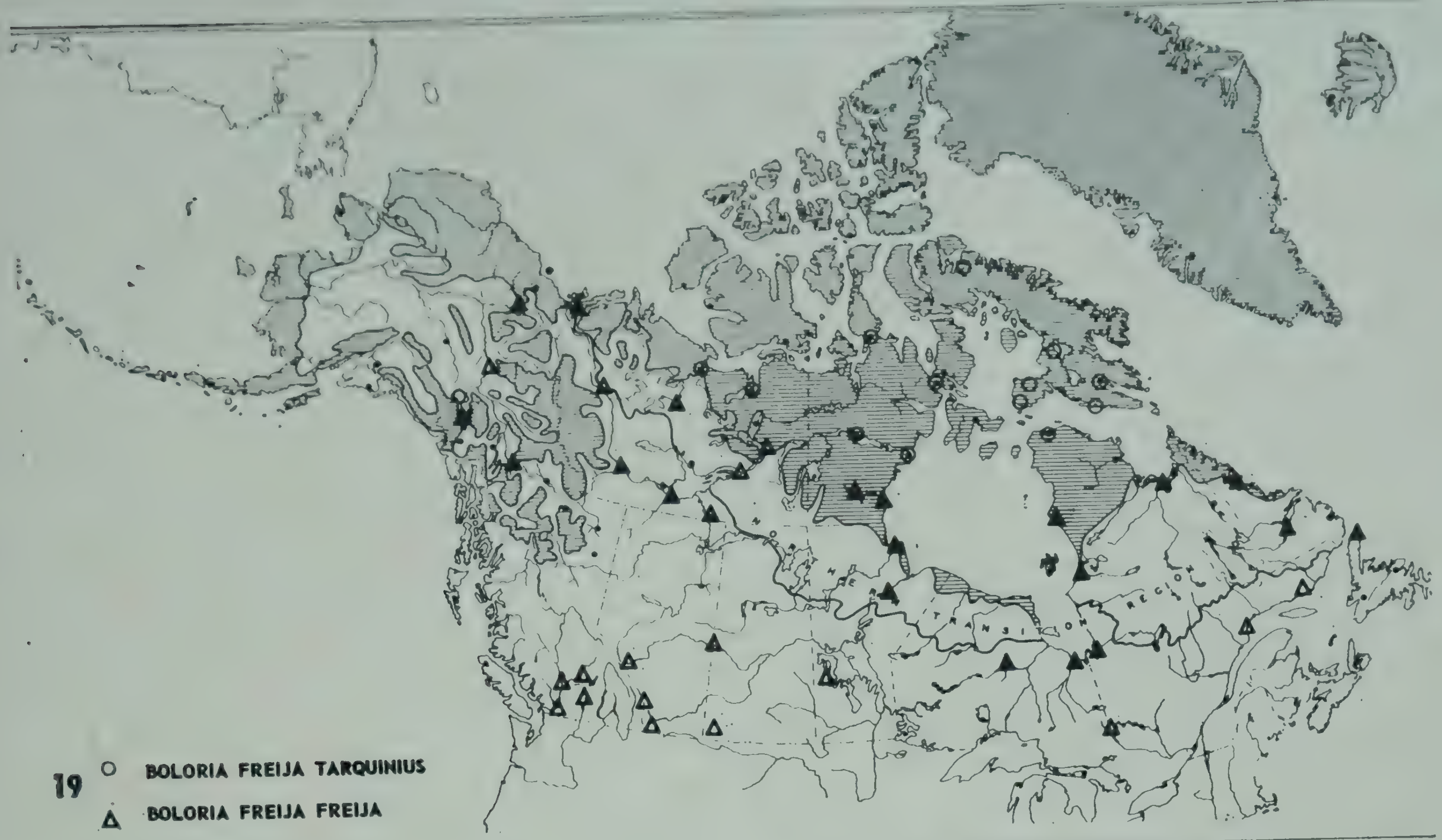
18 ○ BOLORIA FRIGGA GIBSONI
△ BOLORIA FRIGGA SAGA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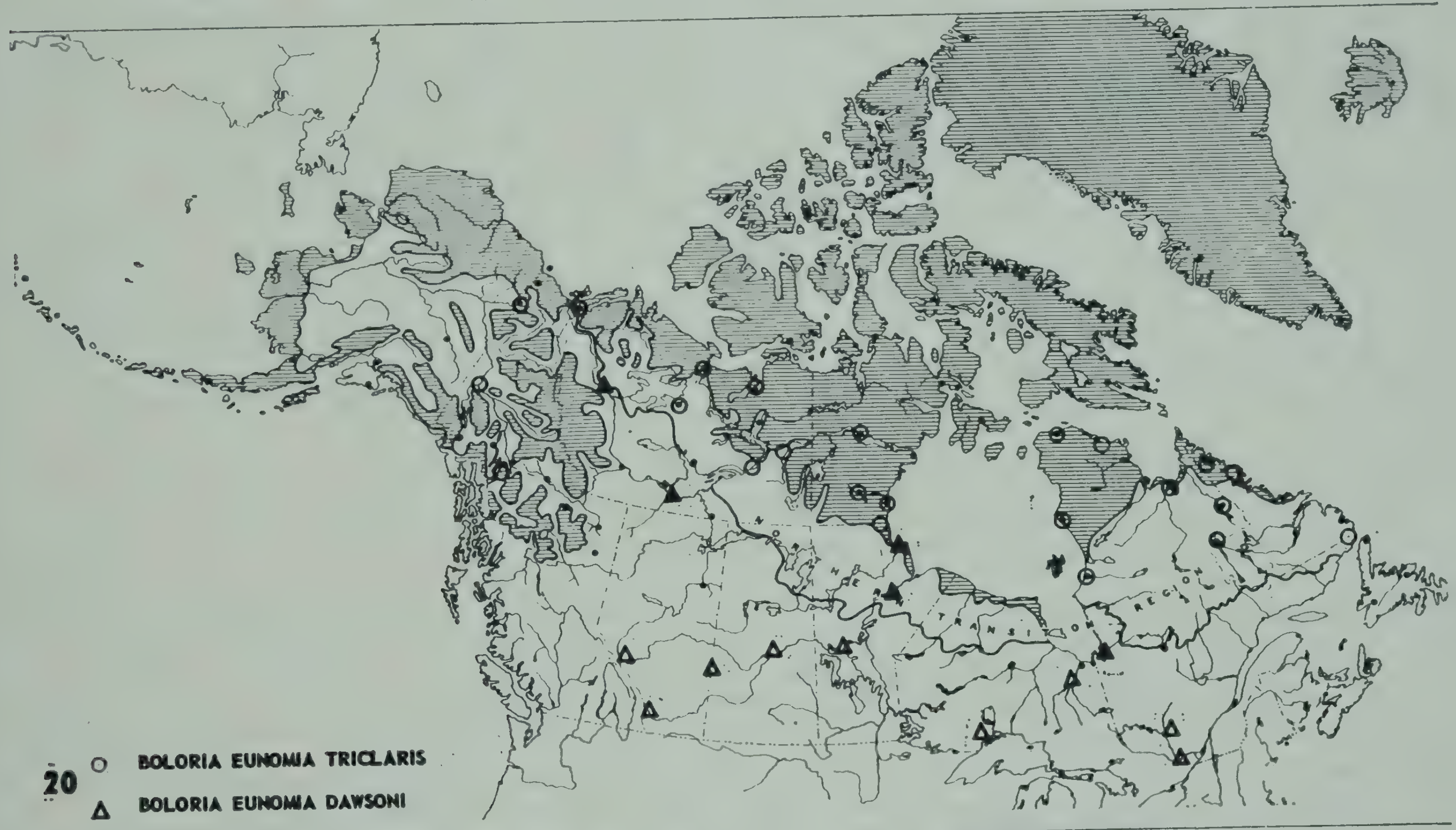
△ BOLORIA FREIJA FREIJA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20 ○ BOLORIA EUNOMIA TRICLARIS
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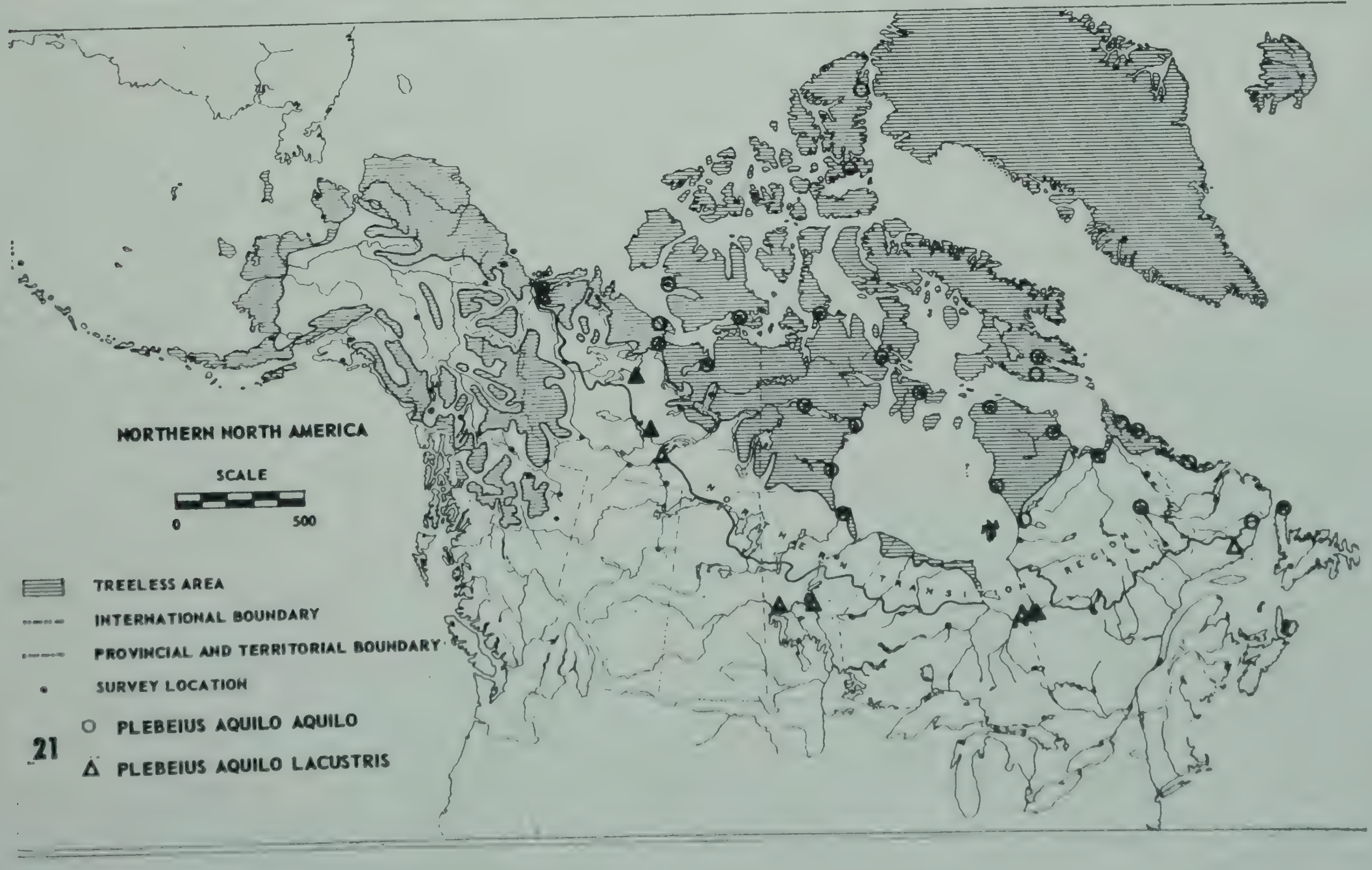
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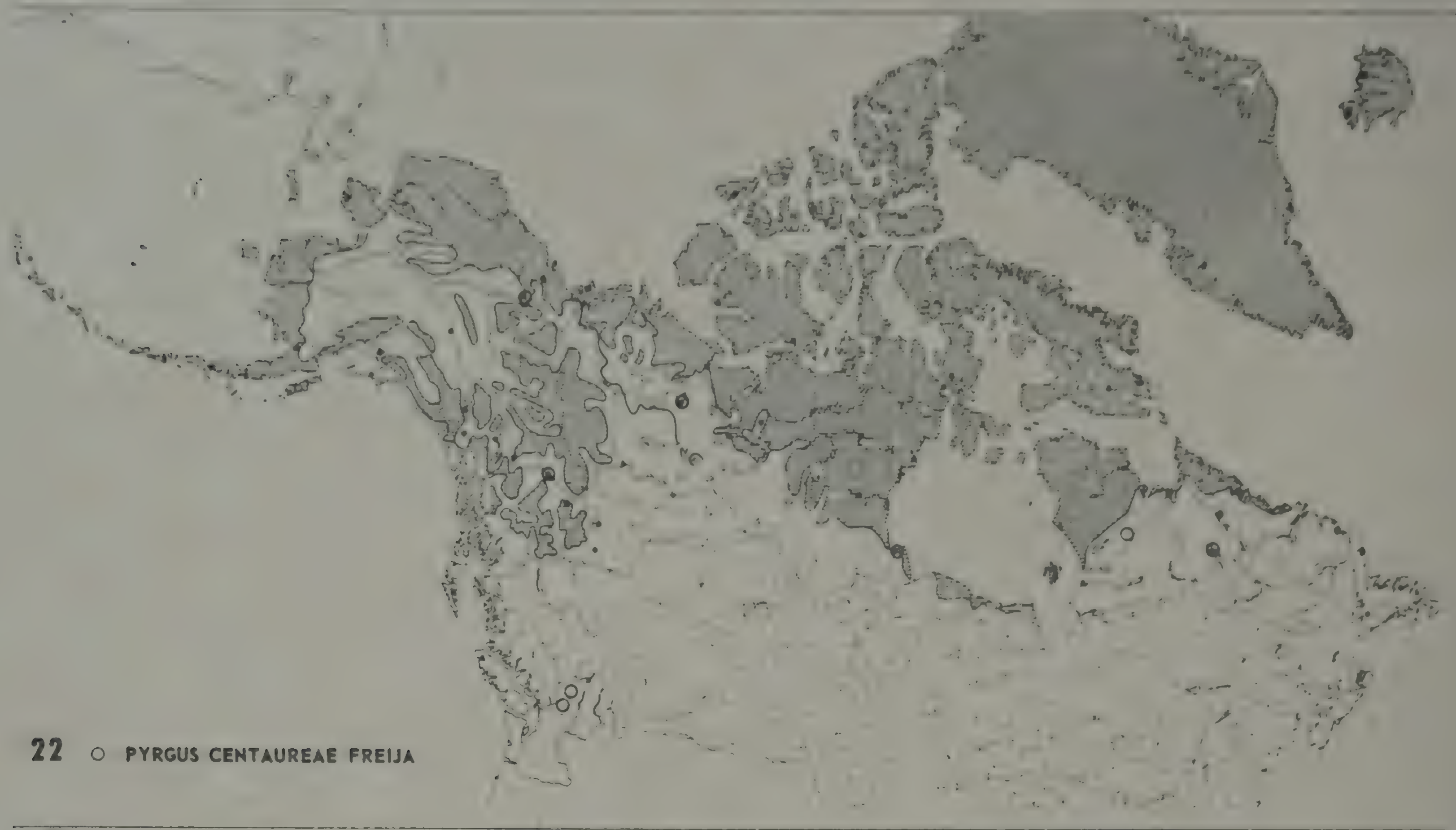
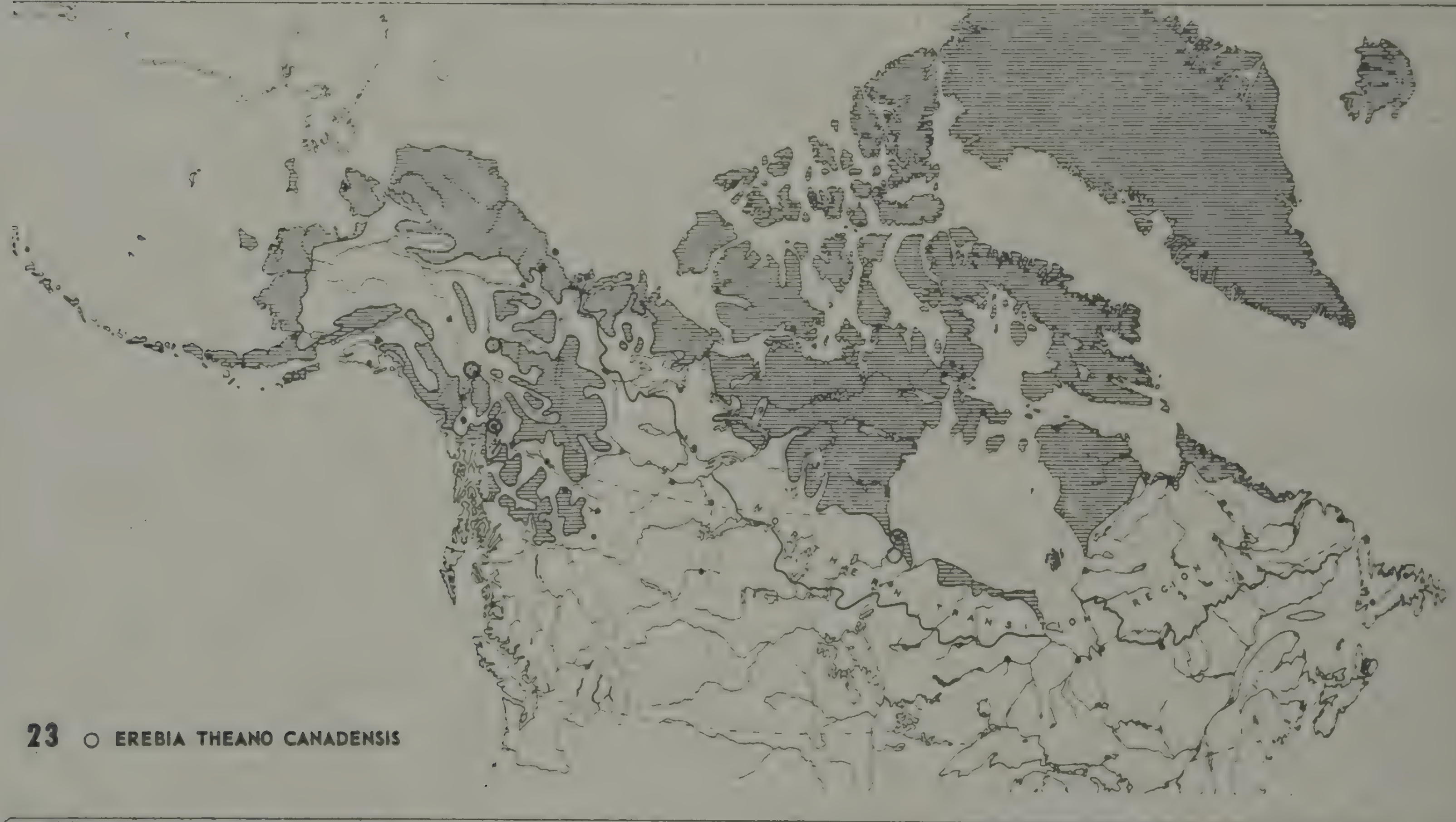
21 ○ PLEBEIUS AQUILO AQUILO
△ PLEBEIUS AQUILO LACUSTRIS



22 ○ PYRGUS CENTAUREAE FREIJA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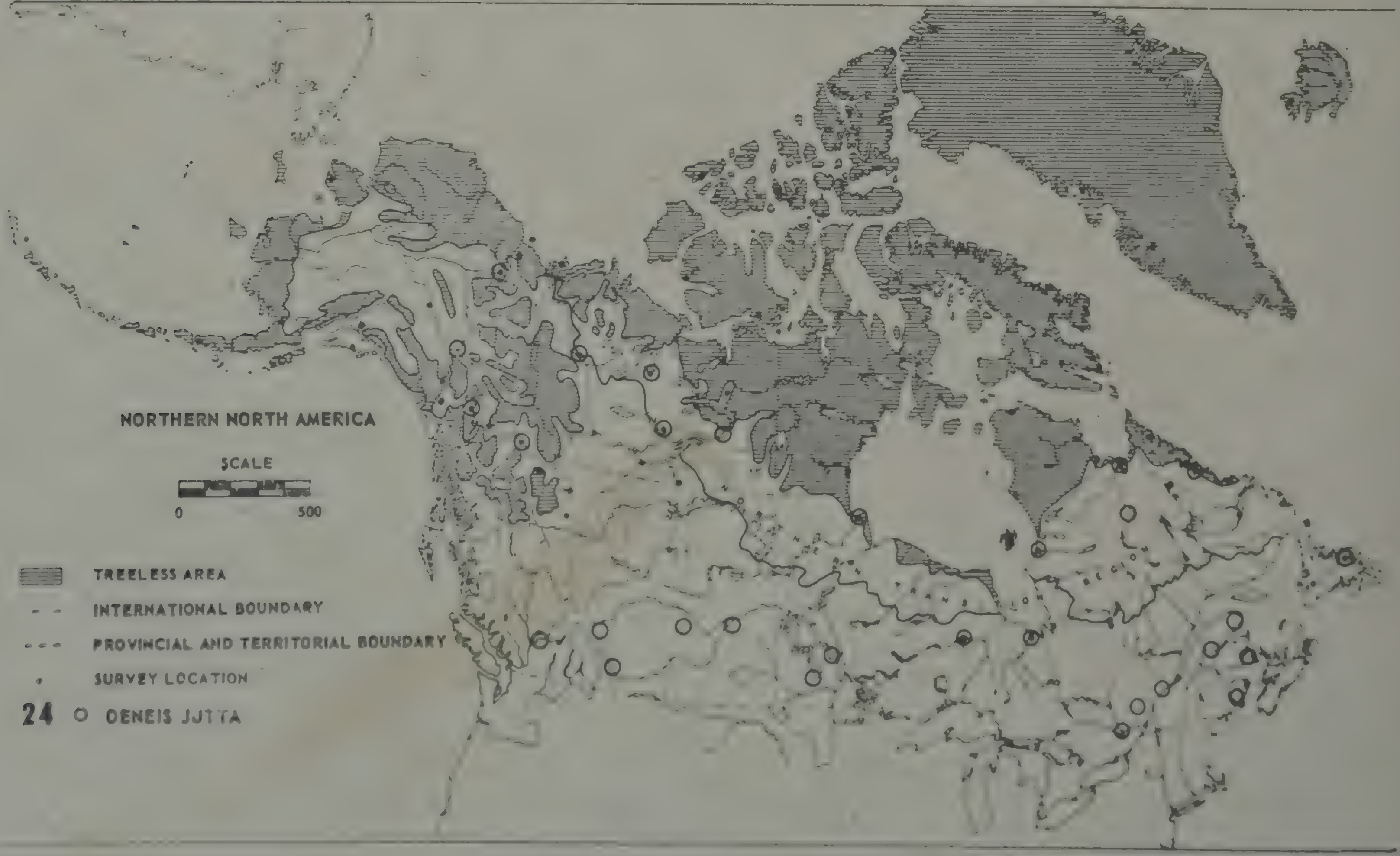
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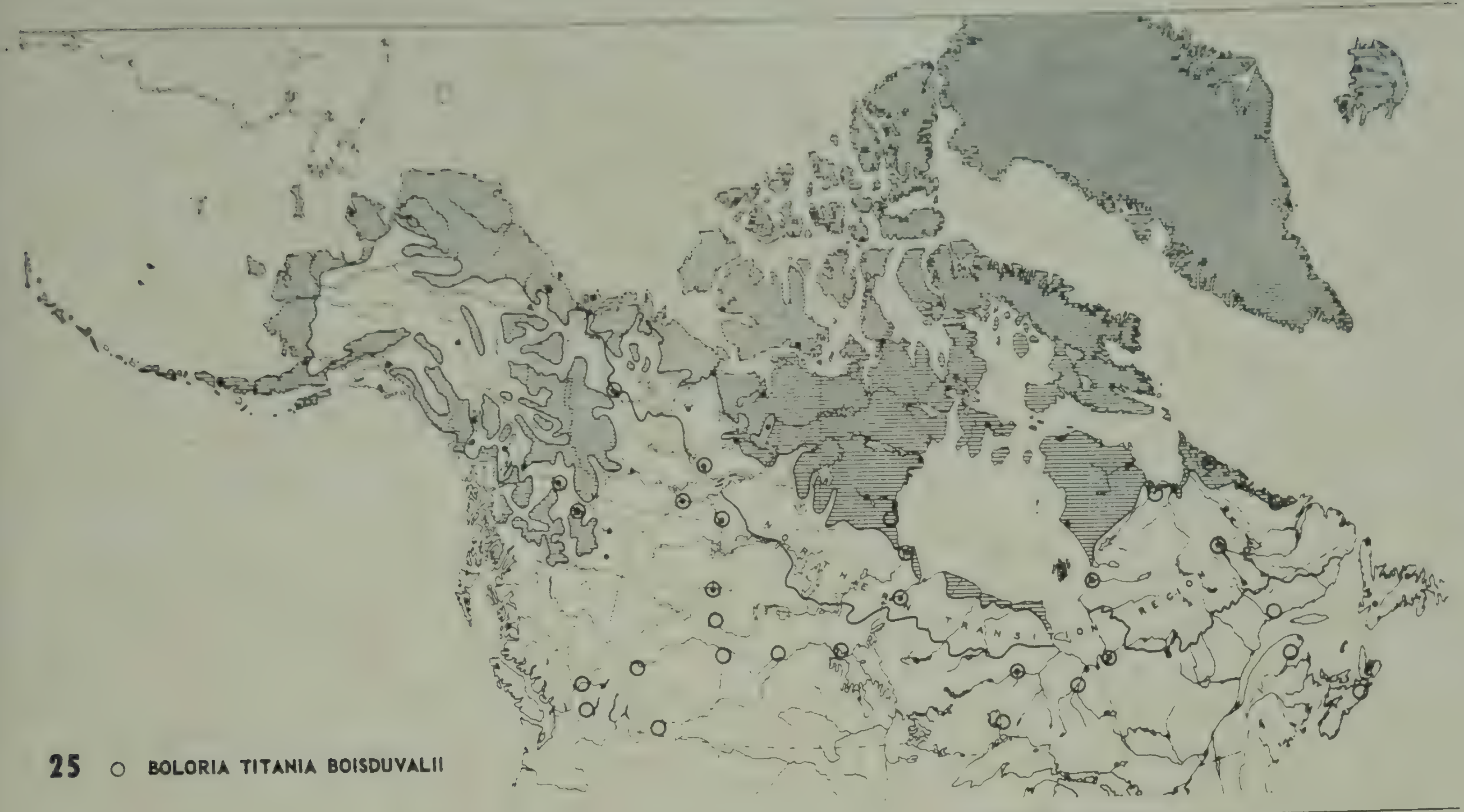
TRANSITION REGION

24 ○ OENEIS JUTTA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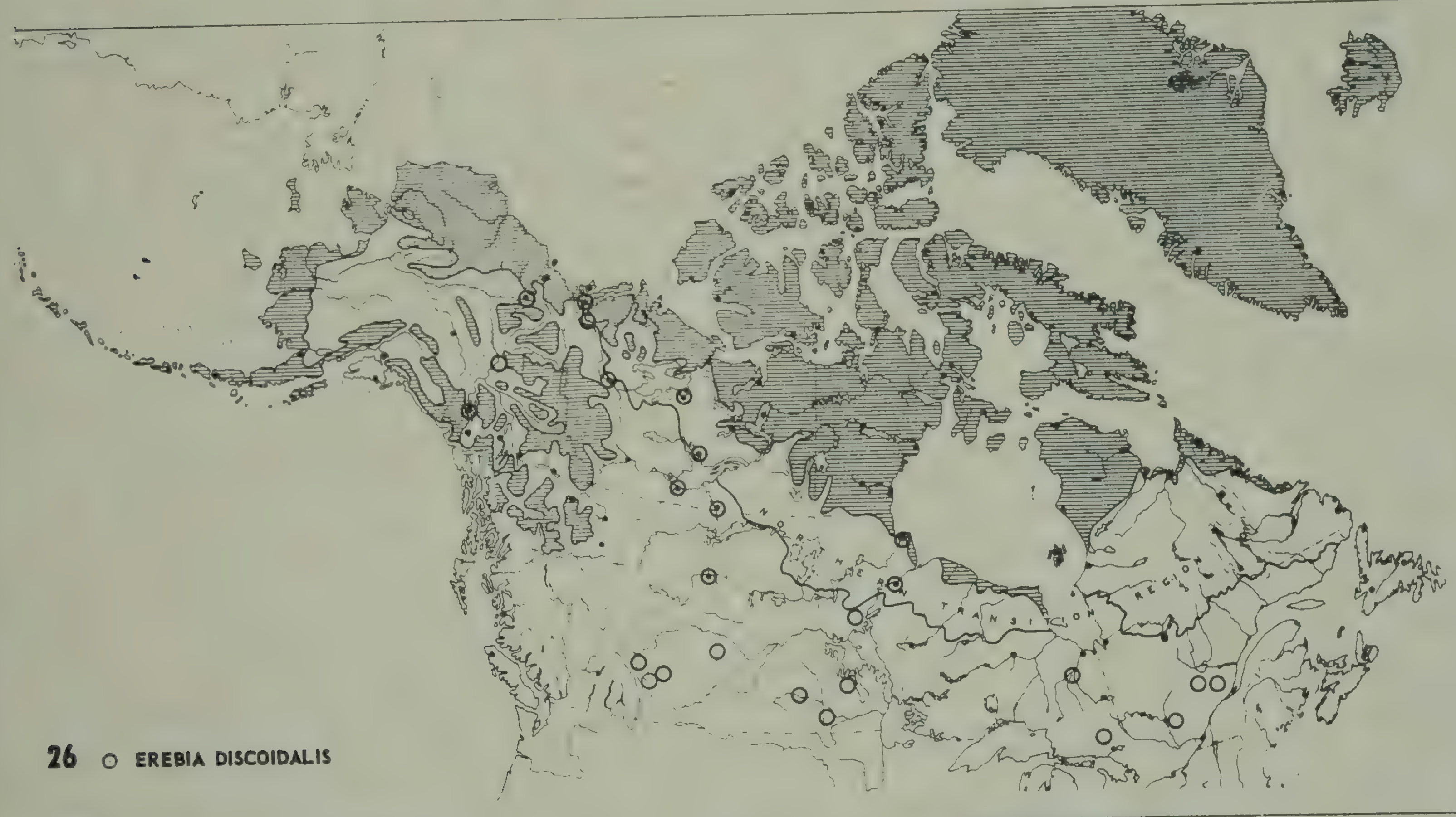
25 ○ BOLORIA TITANIA BOISDUVALII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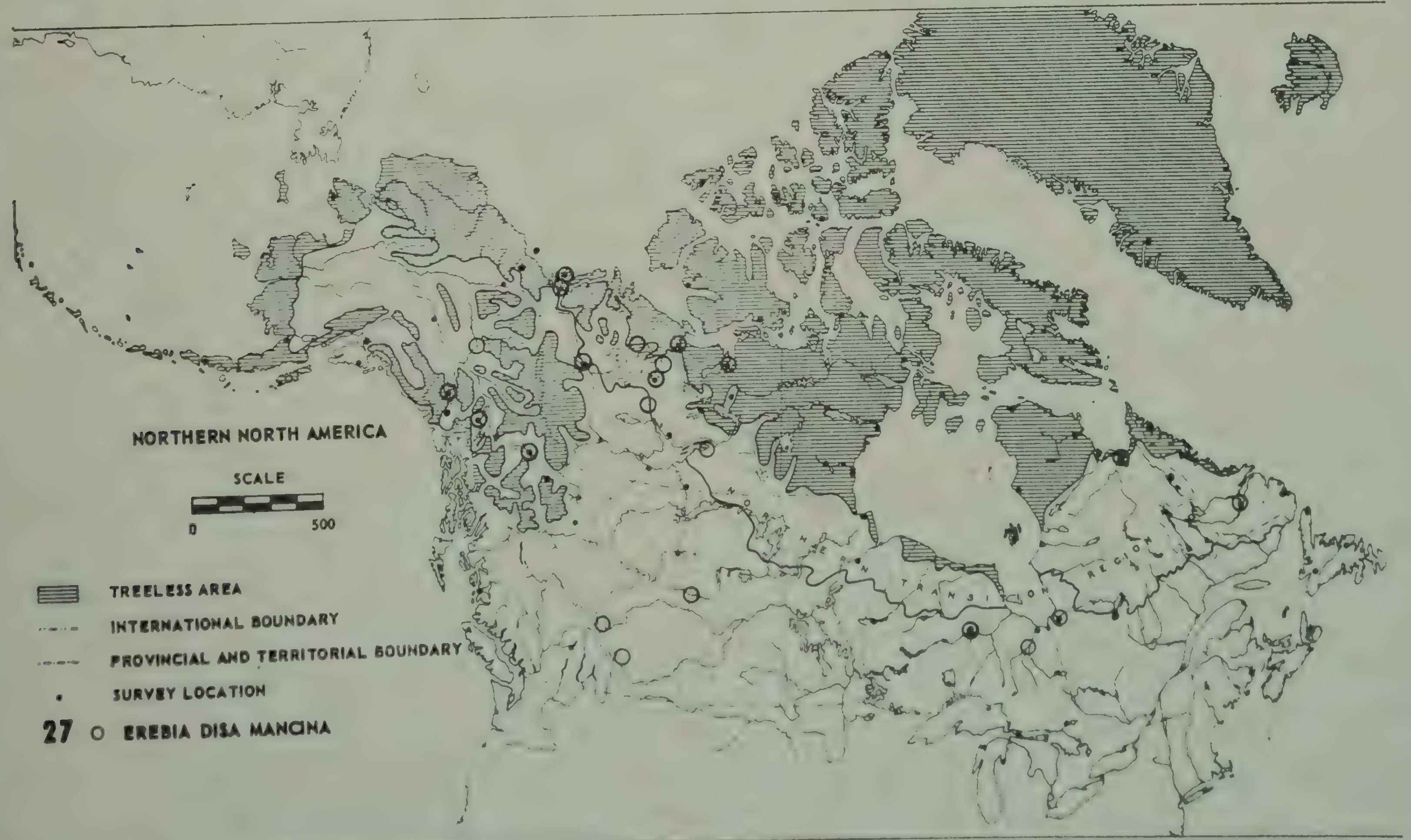
26 ○ EREBIA DISCOIDALIS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27 ○ EREBIA DISA MANCINA

Plebeius aquilo lacustris Free. (Fig. 21) occurs across Canada in the Hudsonian zone (Northern Transition) only, and meets the northern *aquilo aquilo* Bdv. near Aklavik, N.W.T. The few specimens I have seen from Aklavik suggest two quite distinct forms.

Pyrus centaureae freija Warren (Fig. 22) appears to represent another typically Hudsonian transcontinental form. *Erebia theano canadensis* Warren (Fig. 23) may be another Hudsonian species restricted to the Hudsonian region west of Hudson Bay. It apparently occurs very locally and is rarely taken by collectors. More collections are required from different areas to establish the environmental region it inhabits.

The last four species dealt with in this paper occur essentially in the Canadian zone and invade the Hudsonian. They are practically beyond the scope of this paper and represent examples of the blending of distributional patterns in the life zones south of the Arctic. *Oeneis jutta* Hbn. (Fig. 24) occurs in the sphagnum bogs of the Canadian and Hudsonian zones. *Boloria titania boisduvalii* Dup. (Fig. 25) occurs in sphagnum bogs and wet grassy meadows. The distributional pattern of *Erebia discoidalis* Kby. (Fig. 26) suggests a post glacial entry from the north-west, apparently not yet having reached eastern Quebec and the Maritime provinces. The distribution of *Erebia disa mancina* West. (Fig. 27) shows a large gap in Manitoba and most of Saskatchewan. This is probably due to lack of collecting, or it may be correlated with the distributional patterns of *Colias pelidne* Bdv. and *Colias palaeno chippewa* Kby. into eastern and western components.

The distribution of butterflies within the arctic and subarctic regions east of the Cordilleran System show four main patterns:

(1) Those that are indigenous to the arctic only.

(2) Those species that extend from the northern Canadian region through the Hudsonian into the Arctic.

(3) Those that appear to inhabit the Hudsonian Zone only.

(4) Those that occur in both the Canadian and Hudsonian Zones.

These main distributional patterns may be further subdivided into transcontinental, eastern, western, northern or southern sections. The distributions of the 16 wholly arctic species may be summarized as follows:

TRANSCONTINENTAL ARCTIC

Lycaena phlaeas feildeni McLach. (Fig. 6)
Boloria improba Butl. (Fig. 7)
Erebia rossii Curt. (Fig. 8)
Boloria chariclea arctica Zett. (Fig. 9)
Colias hecla Lef. (Fig. 10)
Colias nastes Bdv. (Fig. 11)
Boloria polaris Bdv. (Fig. 12)
Oeneis taygete Geyer (Fig. 15)
Oeneis melissa Fabr. (Fig. 16)
Oeneis polixenes Fabr. (Fig. 17)

WESTERN ARCTIC

Erebia youngi Holl. (Fig. 2)
Boloria pales D. and S. (Fig. 3)
Erebia fasciata Butl. (Fig. 4)
Colias boothii Curt. (Fig. 5)
Colias palaeno chippewa Kby. (Fig. 13)

EASTERN ARCTIC

Colias pelidne Bdv. (Fig. 14)

NORTHERN ARCTIC

Lycaena phlaeas feildeni McLach. (Fig. 6)

MID–ARCTIC

Boloria pales D. & S. (Fig. 3)

SOUTHERN ARCTIC

Erebia fasciata Butl. (Fig. 4)
Colias boothii Curt. (Fig. 5)
Boloria improba Butl. (Fig. 7)
Erebia rossii Curt. (Fig. 8)
Colias nastes Bdv. (Fig. 11)
Colias palaeno chippewa Kby. (Fig. 13)
Colias pelidne Bdv. (Fig. 14)
Oeneis taygete Geyer (Fig. 15)
Oeneis melissa Fabr. (Fig. 16)
Oeneis polixenes Fabr. (Fig. 17)

PAN-ARCTIC

Boloria chariclea arctica Zett. (Fig. 9)
Colias hecla Lef. (Fig. 10)
Boloria polaris Bdv. (Fig. 12)

SOUTHEASTERN ARCTIC RELICTS

Oeneis taygete Geyer (Fig. 15)
Oeneis melissa Fabr. (Fig. 16)
Oeneis polixenes Fabr. (Fig. 17)

Four species are dealt with in this paper that inhabit the Canadian Zone and extend into the Hudsonian. They are all transcontinental in distribution, or almost so. Two of the three Hudsonian Zone species are transcontinental and one is western.

All the factors that have operated, and are operating to restrict the present distribution or environment of the butterfly species of northern Canada are undoubtedly many and complex. Some of the basic factors appear to be (1) the northern limit of trees, (2) temperature, (3) prevailing wind direction during the summer, (4) dispersal in time from the refugia during the Pleistocene, (5) the presence or absence of permafrost and (6) the basic geological formations.

The distributional patterns suggest three main refugia for these butterflies during the Pleistocene period (1) in the Cordilleran system, particularly in the northwest, (2) south of the ice, at least in the Appalachian region and (3) north of the ice in the eastern Queen Elizabeth Islands and Greenland. The western Queen Elizabeth Islands are apparently devoid of Lepidoptera and other insect groups. Either climatic conditions are unfavourable for their existence or sufficient time has not elapsed since the Pleistocene era to enable them to become established in this area.

The butterfly environments in a north-south direction east of the Mackenzie River, change in proportion to the distance. As the environment changes, so does the behaviour. As the behaviour diversifies, the relationship between insect species or populations diverges. Among the northern butterflies, and perhaps other insect groups, the species that inhabit the coniferous or Canadian Zone are not, as a rule, conspecific with those that are indigenous to the arctic region.

DISCUSSION

Paul R. Ehrlich. In Alaska the situation is quite different from Arctic Canada, as there is an extensive area of dwarf birch, willow and/or alder north of, or above, the coniferous forest. This is similar to the situation in the Palaearctic.

Harry K. Clench. The difference between Palaearctic and Nearctic tree-line region may find a correlation in the difference between Europe and North America in pollen samples, the samples in the former showing a distinct tundra stratum, absent or nearly so in samples in North America.

A. B. Klots. Timberline in much of North America shows a rather different aspect from that of arctic Europe, as do the southward North American bogs.

Paul R. Ehrlich. How much of a barrier do you feel the barrenness of the Arctic Rock Desert in the Queen Elizabeth Islands is to the northeastward movement of butterflies to such areas as northeastern Ellesmere?

T. N. Freeman. The prevailing northwest winds during the summer and the general severity of the climate throughout the year no doubt restrict the distribution and spread northeast.

James A. Slater. Could you indicate in general the per cent of species that are holarctic in distribution?

T. N. Freeman. Approximately sixty per cent of the arctic species dealt with in this paper are holarctic and forty per cent are nearctic.

Reece I. Sailer. In view of differences such as length of day, I wonder if the Alpine Arctic areas in southern latitude can properly be included in the Arctic life zone?

T. N. Freeman. Some of these arctic alpine areas can certainly be included in the Arctic life zone as demonstrated by conspecific plants and animals occurring in both areas.

G. J. Kerrich. Is there any evidence that species occurring in high latitudes could not survive in lower latitudes at higher altitudes on account of the shorter length of day?

A. B. KLOTS. The great differences in day length of alpine and arctic have little effect on the insects existing in both, due to the ability of both the insects and suitable food plants to adapt to these differences.

R. B. BENSON. It is impossible to make a sharp division between arctic or alpine regions because alpine regions extend into the arctic in Scandinavia, eastern Siberia and in western North America. It is not wise to say that all the arctic sawflies occurring also in southern alpine regions are necessarily catholic in their food plant; some are restricted to single species of *Salix*.

The Satyrid Butterflies of Northwestern North America (Lepidoptera: Satyridae)

By Cyril F. dos Passos
American Museum of Natural History
New York, N.Y.

INTRODUCTION

The biotic provinces, according to Dice (1943), involved in this paper, are the Aleutian and Sitkan and the north or northwestern parts of the Eskimoan, Hudsonian, Oregonian and Montanian. Generally speaking, the area includes Alaska, the Yukon, British Columbia, and the western part of Alberta.

The work of Dice, supplemented by that of Atwood (1940), give one a good idea of the physical and climatic conditions found in those provinces.

ARCTIC COLLECTING

The earliest collectors of insects were, in fact, explorers of the Arctic regions, who traveled by ship and collected here and there only incidentally as they touched shore. They took very few butterflies, and the exact localities where most of them were captured are often doubtful. To such explorers we are indebted for our first Arctic butterflies,usually species of *Colias*, *Oeneis*, and *Erebia*, that were described by the early workers such as Boisduval, Butler, Curtis, Fabricius, Guérin-Méneville, and Kirby.

Prior to 1900 very little additional collecting of insects had been done in this area, and when done at all it had been mostly in connection with and in subordination to the collecting of mammals. But about that time the late William Jacob Holland, of Pittsburgh, Pennsylvania, began to receive butterflies and moths from Moravian missionaries who had settled in or were traveling around in northwestern America.

Later, with the coming of the airplane and the opening of the Alaska Highway and its tributaries, great impetus was given to collecting, and a number of entomologists succeeded in penetrating the area, but their work was necessarily restricted to the regions along the Highway and roads, and around settlements that they were able to visit. Some of those, such as Smith (1953), who collected along the Highway, made valuable contributions to our knowledge of the insect fauna by having their specimens determined by specialists and publishing the results.

The Canadian Arctic Expedition (1913–1918) and especially the Northern Insect Survey, a joint project of the Defense Research Board, Department of National Defence, and of the Division of Entomology of the Department of Agriculture, Canada (1947–) made valuable contributions to our knowledge of insect fauna of the region. The work done by the latter survey resulted in an enormous collection of Arctic Lepidoptera in the Canadian National Collection at Ottawa. Unfortunately, very few of the results of that survey have been published, and those are fragmentary. It was impossible for the author to examine that collection until shortly before this International Congress of Entomology, so complete advantage of the results obtained in the Satyridae will not appear in this paper.

OUTLINE OF THE STUDY

The genera involved in this study are *Coenonympha*, *Cercyonis*, *Oeneis*, and *Erebia*, they being the only genera of Satyrid butterflies occurring in northwestern North America.

The above-mentioned biotic provinces will now be considered from three points of view, i.e., their physical character, climate, and the Satyrid butterflies inhabiting them. Naturally no hard and fast lines can be drawn separating these provinces, because some frequently overlap due to altitudes and other physical factors. The same is true of the butterflies which are found sometimes in more than one province, and at others partly in one and partly in another. Another problem is the lack of ecological data contained in the original descriptions attached to specimens or published in the literature. Such data, rare before 1913, are now supplied usually by the most advanced collectors.

This paper concludes with a catalogue of the species, including their type localities and some notes relative to apparent misdeterminations, as well as a bibliography of references to their original descriptions and to all papers found which deal with the Satyrid butterflies of the area in question.

The Aleutian Province

The Aleutian province includes the Alaska Peninsula and the string of islands extending southwestward from that Peninsula into the Pacific. The Pribilof Islands to the north in the Bering Sea, and Kodiak Island to the east, are included. This province is treeless, but with many shrubs and flowering plants, and is characterized by much fog and rain. The winters are mild, considering the latitude, and the summers are cool.

Only one Satyrid butterfly has been named from this region, *Coenonympha kodiak* Edwards (1869), now considered conspecific with *Coenonympha mixturata* Alphéraky (1897), which was described from Kamtschatka, Siberia. Munroe (1950) records one butterfly from the Pribilof Islands, but it is not a Satyrid.

The Eskimoan Province

The Eskimoan province includes all the northern treeless parts of North America and the Arctic islands, except those included in the Aleutian province. Near the Arctic Coastal Plain in Alaska rises the Brooks Range to a height of 3000 to 6000 feet. Some collecting has been done on that mountain range, but the records have not been published.

Tundra conditions prevail throughout this area, and except as noted the relief is low. The climate is severe in winter and cool in summer. The amount of precipitation varies from moderate to scant in different parts of the territory.

Three of the four genera discussed in this paper occur in the Eskimoan province, as they do also in all provinces to follow, except the Oregonian and Montanian, where four are found. These are *Coenonympha*, one species, *Oeneis*, four species, and *Erebia*, three species. *Cercyonis* alone is absent.

One subspecies, *Erebia youngi herscheli* Leussler (1935), was described from Herschel Island in the Beaufort Sea. Not much is known about the occurrence of any *Coenonympha* in this area, although *kodiak* should occur in the Eskimoan province, and possibly *mackenziei* Davenport (1936) also, although that name was proposed for an insect taken in the Mackenzie District, which is outside the scope of this paper.

The most northern species of *Oeneis*, i.e., *taygete*, *melissa*, *polixenes*, and *yukonensis*, are or may also be found. *Erebia* is represented by *rossii*, *fasciata*, and *youngi*.

The Sitkan Province

The next province to be considered is the Sitkan, which consists of heavy coastal coniferous forests extending from near Kodiak Island southeastward to the southern boundary of Alaska. This coastal strip includes the eastern coast of Alaska, and touches the southern tip of the Yukon. It is the Alaska Range of Atwood's, which farther south in the Oregonian province becomes the Coast Ranges. In Alaska it rises from 6000 to over 20,000 feet. This province has been little explored by entomologists, because of its rugged mountains and steep coast line and islands, with dangerous shoals and strong tides, except in Mount McKinley National Park, and where there are good harbors with resultant settlements, such as Anchorage, Seward, etc.

Mount McKinley National Park is situated partly in this province and partly in the next one. The author (1949) listed the butterflies then known to exist in that area, and described some of them. The Satyrids listed are *Oeneis mackinleyensis* dos Passos (1949) (emendation), *Erebia rossii gabrieli* dos Passos (1949), *Erebia magdalena mackinleyensis* Gunder (1932) and *Erebia youngi rileyi* dos Passos (1947).

Since that time, through the kindness of Mr. Donald Eff, of Boulder, Colorado, the author has seen one male of *Oeneis melissa gibsoni* Holland (1931) taken at Highway Pass in the Park on July 3, 1954.

An interesting butterfly described from this area is *Oeneis brucei yukonensis* Gibson (1920), which that author suggested may be a species. What appears to be the same thing has been seen also from Indian Point, Siberia, there being a long series in the Carnegie Museum.

THE HUDSONIAN PROVINCE

This is by far the largest of the six provinces involved in this study, because it extends across Canada from the Pacific to the Atlantic Oceans. Insofar as we are concerned, it is bounded on the north by the Eskimoan, on the east by the eastern boundary of the Yukon, on the west by the Aleutian and Sitkan, and on the south by the northern parts of the Oregonian and Montanian provinces.

The Hudsonian province consists of a broad zone of spruce forest, just south of the Eskimoan tundras. It does not cross the Rocky Mountains, and touches the Pacific only on Cook Inlet, Alaska.

Ehrlich (1955) has published an excellent map showing the distribution of *Erebia epipsodea remingtoni* Ehrlich (1952) in this area, as well as in the Montanian province to the south.

In addition to the Satyrids listed from Mount McKinley National Park, there is every reason to believe that one or more species of *Coenonympha* occur in this area. There are present also species of *Oeneis* and *Erebia*, such as *Oeneis taygete fordi* dos Passos (1949) and *Erebia rossii kuskoquima* Holland (1931).

THE OREGONIAN PROVINCE

This province includes British Columbia, west of the Coast Ranges and south of the Sitkan province, the demarcation between the latter two being somewhat arbitrary. It does not concern us south of the Canadian border, although many of the species described from the northern United States occur in this province also.

Much of this province is mountainous and covered with a heavy coniferous forest. It has mild temperatures throughout the year, but the rainfalls are considerable, reaching a maximum in the winter.

Probably the most interesting butterflies found in this province are *Oeneis nevadensis gigas* Butler (1868), the largest of our *Oeneis*, and *Erebia vidleri* Elwes (1898). The former insect seems to occur as far north as Atlin. The latter insect has been recorded only from British Columbia and Washington, where it is found in restricted areas in the Coast Ranges. It is a butterfly without any near relative. *Coenonympha ampelos insulana* McDunnough (1928) was described from Victoria, British Columbia. Some other species will be mentioned in the next heading as common to the Oregonian and Montanian provinces.

THE MONTANIAN PROVINCE

This province, as considered in this paper, includes the southern half of British Columbia to the east of the Oregonian province and the western triangle of Alberta. It consists of the northern part of the Rocky Mountains. The British Columbia Plateau occupies the central part of this province, extending a little west of north and east of south at an average altitude of about 5000 feet from the Canadian line to the Yukon, where it joins the Yukon Plateau and extends to the Bering Sea at an average elevation of about 2000 feet.

The biota of the province is closely related to that of the Coloradan province, which covers the southern Rocky Mountain area. The climate is severe in winter, but less so than that of the Hudsonian.

To the east of the Rocky Mountains are the Great Plains, extending almost to the Arctic Coastal Plain along the Mackenzie River valley. Its elevation averages about 2000 feet. That area is outside the scope of this paper.

Many species described from the northern United States occur in this province also. It includes probably more of the species dealt with than any other province. Those of interest are three *Cercyonis* species, two *Coenonympha*, and many *Oeneis* and *Erebia*. One of the interesting *Oeneis* is the widespread *chryxus* (Doubleday) ("1850–1852" [1849]), which inhabits an area from Colorado to the Gaspé, to James Bay, thence to Churchill and across the continent to Alaska, and south to Colorado and adjoining states. It is one of the most widely distributed species of the genus in North America. No record of *Oeneis jutta reducta* McDunnough (1929) has been seen from north of Montana, but it could occur at low elevations in this province.

SOUTHERN AND EASTERN DISTRIBUTIONS OF THE GENERA

Before concluding, it is interesting to pause and consider, for a moment, the southern and eastern distributions of the genera discussed in this paper.

That investigation shows that *Cercyonis*, which occurs less far north than the others, is represented much farther south than the rest, i.e., to the Mexican border and beyond, two species having been reported from Brazil and Bolivia, although the latter is doubtfully placed in this genus. *Coenonympha* and *Oeneis* both extend into Arizona and New Mexico, and *Coenonympha* into southern California as well, but these do not extend as far south as *Cercyonis*. *Erebia* alone is slightly more restricted in its southern distribution, not occurring south of Colorado. The southern distribution of *Oeneis* and *Erebia* is limited to the Rocky Mountains, and the latter occurs in the Sierra Nevada Mountains also, while *Cercyonis* and *Coenonympha* occur also at lower elevations in the Pacific States, where the latter is double-brooded.

When we turn to the transcontinental distribution of these genera we find that three of them, *Cercyonis*, *Coenonympha*, and *Oeneis* extend across the continent to the Atlantic Ocean, but that *Erebia* is somewhat more restricted. Generally speaking, its distribution ceases somewhere in Quebec in the north, and in Minnesota in the south. There are Ontario records for *Erebia disa* (Thunberg) (1791) and for *Erebia epipsodea* Butler (1868). No *Erebia* has been reported from Newfoundland, New Brunswick, Nova Scotia or Maine. Of course, the lack of any equivalent to the Rocky Mountains in the east accounts, in part, for the fact that no species of *Oeneis* occurs south of New Hampshire, but it is difficult to say why in more northern latitudes *Erebia* is not found farther east, conditions being suitable apparently for an extension of its range to the Atlantic.

CONCLUSIONS

It is evident that the genera discussed in this paper, with the exception of *Cercyonis*, have a wide Holarctic distribution.

We find one species of *Coenonympha*, i.e., *kodiak*, occurring in Siberia as well as Alaska, one species of *Oeneis*, i.e., *jutta* Hübner ("1805" [1805–1806]), occurring in Siberia and Alaska as well as Europe, and another, *yukonensis*, in Alaska and Siberia. It is most probable that other species of the Nearctic *Oeneis* occur in Siberia, but so little is known of the fauna of that region that we can only speculate on the subject.

Warren (1936) recognized two subspecies of *Erebia rossii* (Curtis) (1835) as occurring in Asia, two of *disa* from Europe and Asia, one subspecies of *fasciata* Butler (1868) from Asia as far east as the Bering Sea coast, two subspecies of *discoidalis* (Kirby) (1837) from Siberia, five subspecies of *theano* (Tauscher) (1806) from Europe and Asia, and four subspecies of *callias* Edwards (1871) from Europe and Asia, so that on the whole it will be seen that out of the nine species recorded from our area and one from farther south, about two-thirds of them occur in Europe or Asia. Perhaps this rather complete evidence is due to the fact that *Erebia* has been more thoroughly studied than the other genera involved.

It is highly interesting, but perhaps not very fruitful to speculate concerning the possible origin of these genera.

At present *Cercyonis* has no Palaearctic representative, but it has near relatives in *Minois* Hübner ("1816" [1819]) with which it has sometimes been combined. If we assume that these two genera had a common ancestor, they may have originated in the Palaearctic or Nearctic regions. *Coenonympha* and *Oeneis* may have originated in America, Europe, or Asia, for we find species of those genera on all three continents, and there is a possibility that these genera could have originated on either one. With *Erebia* the case is similar, but slightly different. Although species are found on all three continents, *Erebia* is absent from the eastern part of North America. Does that imply that it must have originated in western America, or Asia, or Europe, and spread eastward to the New World? Who knows whether *Erebia* in North America is a shrinking or expanding entity? Perhaps it once extended to the Atlantic. No positive answer can be given to these questions. As observed above, they are highly interesting speculations. The most plausible theory thus far advanced is that these genera entered North America from Asia near the present Bering Strait, which was than a land bridge.

CATALOGUE OF THE SPECIES OF SATYRIDAE FOUND IN NORTHWESTERN NORTH AMERICA

I. Coenonympha Hübner, "1816" [1819]

1. *kodiak* Edwards, 1869
   k. kodiak Edwards, 1869. Kodiak, [Alaska].
      yukonensis Holland, 1900. Dawson, Yukon Territory, July 1; Eagle City, Alaska, July 14; American Creek, Alaska, July 18 (S. Hall Young).
2. *ampelos* Edwards, 1871
   a. ampelos Edwards, 1871. Oregon.
      gen. vern. *columbiana* McDunnough, 1928. Aspen Grove, B[ritish] C[olumbia], June 15 (P. N. Vroom).
      eunomia Field, 1937. Wilhoit, Oregon, June 6, 1937 (C. W. Herr).
   a. insulana McDunnough, 1928. Victoria, B[ritish] C[olumbia], May 20 (W. Downes).
3. *ochracea* Edwards, 1861. Lake Winnipeg, [Manitoba]; California; Kansas.
   o. mackenziei Davenport, 1936. Nyarling River, Mackenzie Dist[rict], July 4, 1926 (J. Russell).

There are differences of opinion as to how many species of *Coenonympha* occur in North America. Davenport (1941) refers all of them to *tullia* (Müller) (1764); later authors, including Brown (1955), have referred all except *kodiak* to *inornata* Edwards (1861), treating it as a "superspecies" under *tullia*.

Those who base their opinion on the genitalia alone recognize one, *tullia*, or at least two species. Others who place some reliance on the pattern of the insect's wings and its distribution recognize as many as six species. The problem is not too important, but it is easier to handle the names if half a dozen species are recognized.

Bowman's (1951) record of *inornata benjamini* McDunnough (1928) can hardly be included, since that subspecies was described from Waterton Lakes, Alberta, which is in prairie country.

II. Cercyonis Scudder, 1875

1. *pegala* (Fabricius), 1775. In America (Mus. D. Hunter).
   p. boopis (Behr), 1864. Contra Costa, [California], July.
      ariane (Boisduval), 1852, (*partim*). Forests, [California].
2. *silvestris* (Edwards), 1861. California (from H. Behr).
   s. paulus (Edwards), 1879. Nevada (H. K. Morrison).
3. *oetus* (Boisduval), 1869
   o. oetus (Boisduval), 1869. Mountains, [California], July.
      charon (Edwards), 1872. Near Twin Lakes, Upper Arkansas Valley, Colorado, 8000 feet, July, 1871, throughout park and mountain country until September (T. L. Mead).
   o. phocus (Edwards), 1874. Lake Labache [*sic*], British Columbia, 1873 (G. R. Crotch).

Bowman (1951) records *alope nephele* (Kirby) (1837) from Alberta, mostly from prairie country. Doubtless this insect should be referred to *pegala ino* Hall (1924), which is omitted because a lowland subspecies.

Apparently both subspecies of *oetus* occur in our area, but *phocus* occupies higher ground.

III. Oeneis Hübner, "1816" [1819]

1. *uhleri* (Reakirt), 1866. Rocky Mountains, Colorado Terr[itory].
      ab. obscura (Edwards), 1892. [Colorado.]
   u. nahanni Dyar, 1904. Nahanni Mountains, Mackenzie, 2500 feet, July 16, 1903 (Merritt Cary).
      cairnesi Gibson, 1920. White river district, Yukon Territory, lat[itude] 61° 55′, long[itude] 141°, July 16, 1913 (D. D. Cairnes).
2. *nevadensis* (Felder and Felder), "1864–1867" [1867]. Sierra Nevada, California (Lorquin).
      californica (Boisduval), 1869. High mountains, California (Lorquin).
   n. gigas Butler, 1868. Vancouver's Island, [British Columbia].
3. *chryxus* (Doubleday), "1850–1852" [1849]
   c. chryxus (Doubleday), "1850–1852" [1849]. Rocky Mountains, [Alberta], North America.
   c. caryi Dyar, 1904. Smith Landing, Athabasca, June 13, 1903 (Merritt Cary).
4. *alberta* Elwes, 1893
   a. alberta Elwes, 1893. Near Calgary, [Alberta], about May 16 (F. H. Wolley Dod).
5. *taygete* Geyer, [1830]. Labrador.
      bootes (Boisduval), 1832. Cap Nord; Kamtschatka (Eschscholtz); Greenland and Labrador (Sommer).
   t. hanburyi Watkins, 1928. Arctic coast about Coronation Gulf, Grays Bay, July 1–3, 1902 (David Hanbury).
   t. fordi dos Passos, 1949. Kuskokwim River, Alaska (A. Stecker).
   t. edwardsi dos Passos, 1949. San Juan Mountains, Hinsdale County, Colorado, August 4, 1941 (B. Rotger).
6. *mackinleyensis* dos Passos, 1949. (Emendation.) [Mount] McKinley [National] Park, Alaska, June 19, 1932.

7. *jutta* Hübner, "1805" [1805–1806]. Lappland.
    balder Guérin-Méneville, "1829–1844" [1831]. Le Cap Nord, [Norway].
    j. leussleri Bryant, 1935. Base Camp, 25 miles southwest of Aklavik, N[orth] W[est] Terr[itory], July 11, 1931.
    j. alaskensis Holland, 1900. Mountains between Forty-Mile and Mission Creeks, N[orth] E[ast] Alaska, June 20 (S. Hall Young); American Creek, Alaska, July 18 (S. Hall Young).
8. *melissa* (Fabricius), 1775. In insula Terre neuve Americae (Mus. Banks).
    oeno (Boisduval), 1832. Laponie russe; Northern Siberia (Eschscholtz); Labrador (Sommer).
    m. assimilis Butler, 1868. Repulse Bay.
        arctica Gibson, 1920. Bernard Harbour, Northwest Territory, July, 1916 (F. Johanson).
        simulans Gibson, 1920. Bernard Harbour, Northwest Territory, July, 1915 (F. Johanson).
    m. gibsoni Holland, 1931. Kuskokwim Valley, [Alaska].
    m. beanii Elwes, 1893. Laggan, [Alberta], 8–9000 feet, July 15–30 (T. E. Bean).
9. *polixenes* (Fabricius), 1775. In America boreali (Mus. Banks).
    crambis (Freyer), 1845. Lapland.
    p. peartiae (Edwards), 1897. Winter Cove, Cambridge Bay, Victoria Land, lat[itude] 69°, long[itude] 106° (Captain Collinson).
    p. subhyalina (Curtis), 1835. [Boothia Felix], Arctic regions, ?July 18–25, 1830, ?July 14, 1831.
10. *brucei* (Edwards), 1891. Colorado (David Bruce).
    b. yukonensis Gibson, 1920. Klutlan glacier, Yukon Territory, 8200 feet, June 14, 1913 (E. W. Nesham).

Blackmore (1927) includes *nevadensis* in his list. In this paper *gigas*, described from Vancouver's Island, is recognized as a good subspecies, so the nominate subspecies is not included. Blackmore also includes *uhleri*, but the nominate subspecies has not been seen from British Columbia.

IV. EREBIA DALMAN, 1816

1. *vidleri* Elwes, 1898. Mountains above Seton Lake, near Lilloet [*sic*] on Fraser River, British Columbia, July, 1885 (Captain Vidler).
2. *rossii* (Curtis), 1835
    r. rossii (Curtis), 1835. [Boothia Felix], Arctic regions, July 18 and 25, 1830, July 14, 1831.
    r. kuskoquima Holland, 1931. Kuskokwim Valley, [Alaska].
    r. gabrieli dos Passos, 1949. Mount McKinley [National] Park, Alaska, 3500 feet, July 5, 1938 (G. P. Engelhardt).
3. *disa* (Thunberg), 1791. In Lapponia (Magist. Quenzel).
    d. mancinus Doubleday, "1850–1852" [1849]. Rocky Mountains, [Alberta], North America.
        macinus Barnes and Benjamin, 1926. (*lapsus calami.*)
    d. steckeri Holland, 1930. Kuskokwim River, Alaska (A. Stecker).
    d. subarctica McDunnough, 1937. Mackenzie Delta, N[orth] W[est] T[erritory], July 17, 1924 (W. H. B. Hoare).
4. *magdalena* Strecker, 1880. Mountains near Georgetown, Colorado, summer of 1879 (E. T. Owen).
    m. mackinleyensis Gunder, 1932. Sable Pass, [Mount] McKinley National Park, Alaska, June 16, 1932 (Frank Morand).
5. *fasciata* Butler, 1868. Arctic America.
    f. avinoffi Holland, 1930. Kotzebue Sound, Alaska, 1881 (E. W. Nelson).
6. *discoidalis* (Kirby), 1837. Cumberland-house, lat[itude] 54°.
    d. macdunnoughi dos Passos, 1940. (Emendation.) White Horse, Alaska, June 6 and 17, 1923 (J. A. Kusche).
7. *theano* (Tauscher), 1806. In montibus Altaicis, Sibiriae.
    t. alaskensis Holland, 1900. Eagle City, Alaska, July 8–12; American Creek, Alaska, July 18 (S. Hall Young).
8. *epipsodea* Butler, 1868
    e. epipsodea Butler, 1868. Rocky Mountains.
        rhodia Edwards, 1871. Colorado (T. L. Mead).
        ab. brucei Elwes, 1889. Summit County, Colorado, 12,000 feet.
    e. remingtoni Ehrlich, 1952. Dawson, Yukon Territory, June 11, 1916 (J. A. Kusche).
    e. hopfingeri Ehrlich, 1954. Black Canyon, south of Methow, Okanogan County, Washington, 1000 feet, May 24, 1952 (J. C. Hopfinger).
9. *youngi* Holland, 1900
    y. youngi Holland, 1900. Mountains between Forty-Mile and Mission Creeks, N[orth] E[ast] Alaska, July 20 (S. Hall Young).
    y. herscheli Leussler, 1935. Herschel Island, [Yukon Territory in Beaufort Sea, 70° North latitude, 139° West longitude], July 20, 1930 (Owen Bryant).
    y. rileyi dos Passos, 1947. [Mount] McKinley [National] Park, Alaska, June 19, 1932.

REFERENCES

Alphéraky, S. 1897. Lepidopteren aus Kamtschatka, gesammelt von O. Herz. *In* Romanoff, Níkolaí Míkhaílovích, Mémoires sur les Lépidoptères 9: 301–347.
Anderson, E. M. 1904. See British Columbia, Provincial Museum of Natural History, Victoria.
Anderson, E. M. 1915. See British Columbia, Provincial Museum of Natural History, Victoria.
Atwood, W. W. 1940. The physiographic provinces of North America. Boston.

Barnes, W., and F. H. Benjamin. 1926. Check list of the diurnal Lepidoptera of Boreal America. *Bull. Southern California Acad. Sci.* 25: 3–27.

Barnes, W., and F. H. Benjamin. 1926. Notes on diurnal Lepidoptera, with additions and corrections to the recent "List of diurnal Lepidoptera." *Ibid.* 25: 88–98.

Barnes, W., and J. H. McDunnough. 1916. Notes on North American diurnal Lepidoptera. Contributions to the natural history of the Lepidoptera of North America. Vol. 3: 53-152.

Bean, T. E. 1890. The butterflies of Laggan, N.W.T.; account of certain species inhabiting the Rocky Mountains in latitude 51° 25′. *Canadian Ent.* 22: 94–99, 126–132.

Bean, T. E. 1893. *Ibid.* 25: 145–149.

Bean, T. E. 1894. *Ibid.* 26: 155–156.

Behr, H. H. 1864. Notes on Californian Satyrides. *Proc. California Acad. Nat. Sci.* 3: 163–166.

Blackmore, E. H. 1927. Check-list of the Macrolepidoptera of British Columbia (butterflies and moths). Victoria, B.C.

Boisduval, J. B. A. D. de. 1832. Icones historiques des Lépidoptères nouveaux ou peu connus. Paris, vol. 1.

Boisduval, J. B. A. D. de. 1852. Lépidoptères de la Californie. *Ann. Soc. Ent. France*, ser. 2, 10: 275–324.

Boisduval, J. B. A. D. de. 1869. Lépidoptères de la Californie. *Ann. Soc. Ent. Belgique* 12: 1–28, 37–94.

Bowman, Kenneth. 1919. Annotated check list of the Macrolepidoptera of Alberta. Red Deer, Alberta, *The Alberta Natural History Society*, 16 pp.

Bowman, Kenneth. 1921. Annotated check list of the Macrolepidoptera of Alberta—additions, 1919. *Canadian Ent.* 53: 13–14.

Bowman, Kenneth. 1921. Annotated check list of the Macrolepidoptera of Alberta—additions, 1920. *Ibid.* 53: 211–212.

Bowman, Kenneth. 1923. Annotated check list of the Macrolepidoptera of Alberta—additions, 1921. *Ibid.* 55: 71–72.

Bowman, Kenneth. 1924. Annotated check list of the Macrolepidoptera of Alberta. Additions. *Ibid.* 56: 189–191.

Bowman, Kenneth. 1951. An annotated list of the Lepidoptera of Alberta. *Canadian Jour. Zool.* 29: 121–165.

British Columbia, Prov. Mus. of Nat. Hist., Victoria. 1904. Catalogue of British Columbia Lepidoptera. [Compiled by Ernest M. Anderson.] Victoria, B.C.

British Columbia, Prov. Mus. of Nat. Hist., Victoria. 1915. Report of E. M. Anderson on Atlin Expedition, 1914. *In* Report of the Provincial Museum of Natural History for the year 1914. Victoria, B.C., pp. F7–F27.

British Columbia, Department of Agriculture. 1906. Check list of British Columbia Lepidoptera. Victoria, B.C.

Brown, F. M. 1953. The subspecies of *Oeneis alberta* (Lepidoptera, Satyridae). *Amer. Mus. Novitates* 1626: 1–21.

Brown, F. M. 1955. Studies of Nearctic *Coenonympha tullia* (Rhopalocera, Satyridae). *Coenonympha tullia inornata* Edwards. *Bull. Amer. Mus. Nat. Hist.* 105: 359–410.

Bryant, Owen, and R. A. Leussler. 1935. See Leussler, Richard A., and [in part] Owen Bryant.

Buckell, E. R. 1947. A list of the Lepidoptera collected in the Shuswap Lake District of British Columbia by Dr. W. R. Buckell. *Proc. Ent. Soc. British Columbia* 43: 11–21.

Butler, A. G. 1868. Catalogue of diurnal Lepidoptera of the family Satyridae in the collection of the British Museum. London, *British Museum (Natural History)*.

Butler, A. G. 1893. Lepidoptera. *In* Butler, A. G., and W. F. Kirby, List of insects collected by Miss Elizabeth Taylor in western North America in the summer of 1892. *Ann. Mag. Nat. Hist.* 12: 11–18.

Cadbury, 3d, J. W. 1938. Lepidoptera collected in northern British Columbia by Miss Josephine de N. Henry. Part 1, Rhopalocera. *Proc. Acad. Nat. Sci. Philadelphia* 89: 387–413.

Cary, Merritt, 1906. On the diurnal Lepidoptera of the Athabaska and Mackenzie region, British America. *Proc. U.S. Natl. Mus.* 31: 425–457.

Chapman, T. A. 1898. A review of the genus *Erebia*, based on an examination of the male appendages. *Trans. Ent. Soc. London*, 209–239.

Clark, A. H. 1935. Arctic butterflies. *Smithsonian Report* for 1934: 267–296.

Cockle, J. W. 1910. Notes on a few butterflies found at Kaslo and in northern British Columbia. *Canadian Ent.* 42: 203–204.

Cockle, J. W. 1915. Notes on the habits of some Lepidoptera. *Proc. Ent. Soc. British Columbia* (new ser.) 5: 91–94.

Curtis, John. 1835. Insects. *In* Ross, John, Narrative of a second voyage in search of a north-west passage, and of a residence in the Arctic regions during . . . 1829–33 . . . London.

Dalman, J. W. 1816. Forsok till systematisk Uppstållning af Sveriges Fjårilar. *Kongliga Svenska Vetenskaps-Akademien, Handlingar*, pp. 48–101, 199–225.

Davenport, D. 1936. A new American *Coenonympha* (Lepid. Satridae). *Canadian Ent.* 68: 79.

Davenport, D. 1941. The butterflies of the satyrid genus *Coenonympha*. *Bull. Mus. Comparative Zool.* 87: 213–349.

Dice, L. R. 1943. The biotic provinces of North America. Ann Arbor.

Dod, F. H. W. 1908. *Argynnis astarte*, Doubl.-Hew., and other high mountain butterflies. *Ent. News* 19: 108–114.

Dod, F. H. W. 1908. Further notes on Alberta Lepidoptera. *Ibid.* 19: 124–125.

dos Passos, C. F. 1939. A catalogue of the original descriptions of the Rhopalocera found north of the Mexican Border. Part Two. The Satyridae. *Bull. Cheyenne Mountain Mus.* 1(2): S-1–S-14.

dos Passos, C. F. 1940. A new subspecies of *Erebia discoidalis* Kirby (Rhopalocera: Satyridae). *Amer. Mus. Novitates* 1053: 1–2.

dos Passos, C. F. 1947. *Erebia youngi* Holland, its subspecies and distribution (Lepidoptera, Satyridae). *Ibid.* 1348: 1–4.

dos Passos, C. F. 1949. New butterflies from Mount McKinley National Park, Alaska, with a review of *Erebia rossii* (Rhopalocera, Satyridae). *Ibid.* 1389: 1–17.

dos Passos, C. F. 1949. The distribution of *Oeneis taygete* Geyer in North America with descriptions of new subspecies (Lepidoptera, Satyridae). *Ibid.* 1399: 1–21.

Doubleday, E., and [in part] J. O. Westwood. [1850–1852 and 143–144 pp.] 1846–1852. The genera of diurnal Lepidoptera: . . . London.

Dyar, H. G. 1900. Papers from the Harriman Alaska expedition. XII. Entomological results (6): Lepidoptera. *Proc. Washington Acad. Sci.* 2: 487–501.

Dyar, H. G. 1904. The Lepidoptera of the Kootenai District of British Columbia. *Proc. U.S. Natl. Mus.* 27: 779–938.

Dyar, H. G. 1904. Two new forms of *Oeneis* Huebner. *Proc. Ent. Soc. Washington* 6: 142.

Edwards, W. H. 1861. Descriptions of certain species of diurnal Lepidoptera, found within the limits of the United States and of British America. *Proc. Acad. Nat. Sci. Philadelphia* 13: 160–164.

Edwards, W. H. 1866. On certain North American species of *Satyrus*. *Proc. Ent. Soc. Philadelphia* 6: 195–200.

Edwards, W. H. 1869. Descriptions of new species of diurnal Lepidoptera found within the United States. *Trans. Amer. Ent. Soc.* 2: 369–376.

Edwards, W. H. 1871. *Ibid.* 3: 205–216.

Edwards, W. H. 1871. Descriptions of new species of North American butterflies. *Ibid.* 3: 266–277.

Edwards, W. H. 1872. Descriptions of new species of diurnal Lepidoptera found within the United States. *Ibid.* 4: 61–70.

Edwards, W. H. 1872. List of species of butterflies collected by Campbell Carrington and William B. Logan, of the Expedition, in 1871. Preliminary report of the United States Geological Survey of Montana and portions of adjacent territories . . . Washington, pp. 466–467.

Edwards, W. H. 1874. Descriptions of new species of diurnal Lepidoptera found in North America. *Trans. Amer. Ent. Soc.* 5: 13–19.

Edwards, W. H. [1874]–1897. The butterflies of North America: with colored drawings and descriptions. Boston and New York.

Edwards, W. H. 1879. Insects. Diurnal Lepidoptera. *Bull. U.S. Natl. Mus.* 15: 155–157.

Edwards, W. H. 1879. Descriptions of new species of butterflies collected by Mr. H. K. Morrison, in Nevada, 1878. *Canadian Ent.* 11: 49–56.

Edwards, W. H. 1880. On certain species of *Satyrus*. *Ibid.* 12: 21–32, 51–55, 90–94, 109–115.

Edwards, W. H. 1885. Description of a new species of *Chionobas* from British America. *Ibid.* 17: 74–75.

Edwards, W. H. 1887. Part IV. Insects. *In* Nelson, E. W. Report upon the natural history collections made in Alaska between . . . 1877 and 1881 . . . Washington, pp. 323–330.

Edwards, W. H. 1891. Description of a new species of *Erebia*, and notes on the so-called Chionobas Bore of Colorado. *Canadian Ent.* 23: 31–33.

Ehrlich, P. R. 1952. The distribution and subspeciation of *Erebia rossii* Curtis (Lepidoptera: Satyridae). *Trans. Amer. Ent. Soc.* 78: 75–88.

Ehrlich, P. R. 1952. A new subspecies of *Erebia epipsodea* Butler (Lepidoptera: Satyridae). *Ent. News* 63: 225–231.

Ehrlich, P. R. 1954. Two new subspecies of *Erebia epipsodea* Butler (Lepidoptera: Satyridae). *Jour. Kansas Ent. Soc.* 27: 80.

Ehrlich, P. R. 1954. Notes on *Erebia rossii* Curtis (Lepidoptera: Satyridae). *Ent. News* 65: 225–227.

Ehrlich, P. R. 1955. The distribution and subspeciation of *Erebia epipsodea* Butler (Lepidoptera: Satyridae). *Univ. Kansas Sci. Bull.* 37: 175–194.

Ehrlich, P. R. 1956. Ecological observations on *Erebia* (Lepidoptera: Satyridae) in northwestern America. *Ent. News* 67: 29–36.

Elwes, H. J. 1889. Notes on the genus *Erebia*. *Trans. Ent. Soc. London*, pp. 317–342.

Elwes, H. J. 1898. A revision of the genus *Erebia*. *Ibid.*: 169–207.

Elwes, H. J. 1899. On the Lepidoptera of the Altai Mountains. *Ibid.*: 295–367.

Elwes, H. J. 1903. On a collection of Lepidoptera from Arctic America. *Ibid.*: 239–243.

Elwes, H. J., and [in part] J. Edwards. 1893. A revision of the genus *Oeneis*. *Trans. Ent. Soc. London*, pp. 457–481.

Fabricius, J. C. 1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburg and Leipzig.

Felder, Cajetan von, and Rudolf Felder 1864–1875. Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859. Vienna.

Field, W. D. 1937. A new seasonal form of *Coenonympha ampelos* Edwards (Lepid.: Satyridae). *Canadian Ent.* 69: 249–250.

Freeman, T. N. 1951. Northern Canada and some northern butterflies. *Lep. News* 5: 41–42.

Freyer, C. F. 1845. Neuere Beiträge zur Schmetterlingskunde mit Abbildungen nach der Natur. Augsburg. Vol. 5, pp.]4] & 166, pls. 385–480.

Geddes, J. G. 1883. List of diurnal Lepidoptera collected in the northwest territory and the Rocky Mountains. *Canadian Ent.* 15: 221–223.

Geyer, Carl [1827–1838]. *In* Hübner, Jacob, Sammlung exotischer Schmetterlinge. Augsburg, vol. 3.

Gibson, A. 1920. The Lepidoptera collected by the Canadian Arctic expedition, 1913–18 . . . Report of the Canadian Arctic Expedition 1913–1918, vol. 3: Insects Part I: Lepidoptera.

Guérin-Méneville, F. E. 1829–1844. Iconographie du Règne Animal de G. Cuvier. . . . Paris and London vol. 3.

Gunder, J. D. 1932. New Rhopalocera (Lepidoptera). *Canadian Ent.* 64: 276–284.

Hall, G. C. 1924. Notes on *Polygonia j-album*, *Cercyonis alope*, *Phyciodes tharos*, *Heodes epixanthe* and *Euphydryas gilletti*. *Jour. N.Y. Ent. Soc.* 32: 109–111.

Harvey, R. V. [n.d.] A guide to some of the butterflies of British Columbia. Thomson Stationery Co.

Herz, Otto. 1898. Reise nach Nordost-Sibirien in das Lenagebiet in den Jahren 1888 und 1889 nebst einem Verzeichnisse der dort erbenteten Macrolepidopteren. *Deutsche Ent. Zeitschr. "Iris"* 11: 209–265.

Holland, W. J. 1898. The butterfly book. New York.

Holland, W. J. 1900. Alaska insects. Parts I–II. *Ent News* 11: 381–389, 416–423.

Holland, W. J. 1930. New species of *Erebia* (Lepidoptera: Satyridae). *Trans. Amer. Ent. Soc.* 56: 149–153.

Holland, W. J. 1931. The butterfly book. New and thoroughly revised edition. Garden City, New York.

Holland, W. J., and A. Avinoff. 1935. The Lepidoptera collected by G. M. Sutton on Southampton Island. Rhopalocera. *Mem. Carnegie Mus.* 12: (2): 3–34.

Hübner, J. [1799–1838]. Sammlung europäischer Schmetterlinge. Augsburg Main Zeifer text and [vol. 1].

Hübner, J. 1816–[1826]. Verzeichniss bekannter Schmettlinge [*sic*]. Augsburg.

Johnston, E. C. 1950. Lepidoptera of the Pribilof Islands, Alaska. *Lep. News* 4: 27–30.

Jones, J. R. J. L. 1951. An annotated check list of the Macrolepidoptera of British Columbia. *Occas. Paper No. 1, Ent. Soc. British Columbia.*

Kirby, W. 1837. The insects. *In* Richardson, J., W. Swainson, and W. Kirby, Fauna Boreali-Americana. Norwich, vol. 4.

Lederer, J. 1853. Lepidopterologisches aus Sibirien. *Verh. zool.-bot. Ges. Wien* 3: 351–386.

Leussler, R. A. 1916. A new variety of *Satyrodes canthus* from Nebraska (Lep.). *Ent. News* 27: 99–100.

Leussler, R. A., and [in part] Owen Bryant. 1935. Notes on the diurnal Lepidoptera of the Canadian Arctic collected by Owen Bryant in the summers of 1929 to 1932. *Bull. Brooklyn Ent. Soc.* 30: 1–10, 42–62, 115–118.

Matsumura, S. 1925. An enumeration of the butterflies and moths from Saghalien, with descriptions of new species and subspecies. *Jour. College Agric. Sapporo* 15: (3): 83–196.

Matsumura, S. 1927. A list of the butterflies of Corea, with description of new species, subspecies and aberrations. *Insecta Matsum.* 1: 159–170.

McDunnough, J. H. 1922. Notes on the Lepidoptera of Alberta. *Canadian Ent.* 54: 134–141.

McDunnough, J. H. 1927. The Lepidoptera of the Seton Lake Region, British Columbia. *Ibid.* 59: 152–162, 193–199, 207–214, 239–246, 266–277.

McDunnough, J. H. 1928. Notes on Canadian diurnal Lepidoptera. *Ibid.* 60: 266–275.

McDunnough, J. H. 1929. Notes on some diurnal Lepidoptera from Yellowstone Park and the adjacent regions of Montana. *Ibid.* 61: 105–107.

McDunnough, J. H. 1937. Critical notes on the Canadian species of the genus *Erebia* (Lepid.). *Ibid.* 69: 14–18.

Müller, O. F. 1764. Fauna Insectorum Fridrichsdalina, sive methodica descriptio Insectorum agri Fridrichsdalensis cum characteribus genericis et specificis, . . . Copenhagen and Leipzig.

Munroe, E. G. 1950. The occurrence of a butterfly in the Pribilof Islands. *Lep. News* 4: 44.

Nordström, F. 1928. Entomologische Ergebnisse der schwedischen Kamtschatka-Expedition, 1920–22. Lepidoptera. I. Diurna. *Arkiv Zool. Stockholm* 19 (21): 5–10.

Phair, A. W. A. [1919]. Three years collecting in the Lillooet District. *Proc. Ent. Soc. British Columbia* 12 (syst. ser.): 34–36.

Reakirt, T. 1866. Coloradian butterflies. *Proc. Ent. Soc. Philadelphia* 6: 122–151.

Remington, Jr., P. S. [1953]. Collecting along the Alaska highway. *Lep. News* 6: 103–106.

Russell, J. 1910. Butterfly collecting near Hope, British Columbia. *Canadian Ent.* 42: 224–227.

Scudder, S. H. 1865. Revision of the hitherto known species of the genus *Chionobas* in North America. *Proc. Ent. Soc. Philadelphia* 5: 1–28.

Scudder, S. H. 1868. Report upon a collection of diurnal Lepidoptera made in Alaska by the Scientific Corps of the Russo-American Telegraph Expedition under the direction of Lieut. W. H. Dall. *Proc. Boston Soc. Nat. Hist.* 12: 42–46.

Scudder, S. H. 1875. Synonymic list of the butterflies of North America, north of Mexico. *Bull. Buffalo Soc. Nat. Sci.* 2: 233–269.

Skinner, H. 1899. Notes on butterflies, with descriptions of new species. *Ent. News* 10: 111–113.

Skinner, H. 1900. Revision of the American species of the Genus *Coenonympha. Trans. Amer. Ent. Soc. Philadelphia* 26: 299–309.

Smith, M. E. 1953. More butterflies from Alaska and the highway. *Lep. News* 7: 123–126.

Strecker, F. H. H. 1880. Descriptions of some new species and varieties of North American Lepidoptera. *Bull. Brooklyn Ent. Soc.* 3: 33–36.

Tauscher, A. M. 1806. Lepidopterorum Russiae indigenorum observationes sex. *Mem. Soc. Imp. Nat. Moscow*, vol. 1.

Tauscher, A. M. 1811. Lepidopterorum Novorum Russiae indigenorum observationes sex. *Ibid.* [second edition] vol. 1: 174–179.

Thunberg, C. P. 1791. Dissertatio entomologica. Sistens insecta Suecica. Upsala.

Venables, E. P. 1910. Note on *Chionobas gigas* Butler. *Canadian Ent.* 42: 228.

Warren, B. C. S. 1936. Monograph of the genus *Erebia*. London.

Watkins, H. T. G. 1928. New satyrid butterflies. *Ann. Mag. Nat. Hist.*, ser. 10, 1: 615–618.

White, A. 1851. List of insects taken by Sir John Richardson and John Rae, Esq., in Arctic North America. *In* Richardson, J., Arctic searching expedition. New York. vol. 2.

Whitehouse, F. C. 1918. Popular and practical entomology. A week's collecting on Coliseum Mountain, Nordegg, Alta. *Canadian Ent.* 50: 1–7.

Winn, A. F. 1912. Lepidoptera from Yukon Territory. *Canadian Ent.* 44: 213–216.

Problems of Arctic-Alpine Insect Distribution as Illustrated by the Butterfly Genus *Erebia* (Satyridae)

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ABSTRACT

An account is given of the distribution and ecology of the nearctic species of Erebia *with special emphasis on comparison of the vertical distributions of the species in the montane areas of Alaska and the Yukon Territory with their horizontal distributions in the eastern Arctic and Subarctic. Possible factors limiting distributions are discussed as well as intrinsic and extrinsic barriers to dispersal.*

The study of arctic or alpine animals presents the ecologist or zoogeographer with rather unique advantages and disadvantages. Weighing heavily on the credit side of the ledger are the relative simplicity of ecosystems encountered in these areas, and the relative uniformity of the treeless habitat. A seldom mentioned but very real advantage is that the worker studying arctic or alpine material need ordinarily deal with the intrusive influences of only one other major fauna, that of the boreal forest or its southern montane equivalent. In contrast an investigator in more temperate areas usually must deal with two or more adjacent faunas.

On the debit side one must place the great expense and technical difficulties of working in most arctic or alpine regions, the very short working seasons, and the resultant lack of life history information and museum material for systematic studies. However, with progressive opening of arctic areas these difficulties are being reduced, and it seems apparent that more and more ecologists and population geneticists, who must study natural situations of appalling complexity, will turn to the North for material.

This paper is based on five seasons of field work in northern Canada and Alaska, however the majority of the included data were collected during the summer of 1955, when a grant from the Sigma Xi-Resa research fund permitted the author to spend six weeks in Alaska, the Yukon, and northwestern British Columbia surveying *Erebia* ecology and distribution (see Ehrlich, 1956).

One interesting problem in the zoogeography of boreal insects concerns their vertical distribution in subarctic mountains relative to their north-south distribution in non-montane areas. Of the 11 nearctic species of *Erebia*, *E. fasciata* Butler is the most typically arctic. Figure 1 is a map showing the distribution of *fasciata* on which the northern limit of the forest is indicated by the dotted line. In the eastern arctic *fasciata* does not occur as far south as the northern limit of the trees; it has not been found at treeline at Churchill, Manitoba, a locality which has been heavily collected. True to form, in Alaskan and Yukon montane situations it was found only above treeline in moist tundra areas.

Erebia rossii Curtis (Fig. 2) on the other hand has been recorded at The Pas, Manitoba, where collecting has shown it to be infrequent, and also at Gillam, Manitoba, where to the author's knowledge only one specimen has been taken. Both of these localities are far south of the northern limit of the boreal forest, although large tundra-like areas exist near Gillam. It is also evidently widespread in the mountains of northern British Columbia. Despite these records *rossii* has long enjoyed a reputation as a butterfly found only in the far arctic. Twenty years ago this impression was so strong that the first British Columbian specimen, a typical *rossii*, was listed as *Erebia disa* Thunberg in a publication (Cadbury, 1938) in which two pages are consumed justifying the misidentification. However, I was still quite surprised to find *rossii* most common in the Alaskan mountains in open areas well below treeline, as in the Teklanika River valley in McKinley National Park. On the Steese Highway it was taken amid swarms of *Papilio machaon* L. and *Pieris napi* L., the former being typical of the Hudsonian and the latter of the Canadian Life zone.

Erebia disa (Fig. 3) has usually been found associated with spruce woods or bogs. Occasionally *disa* will be found in the open, as it was near treeline at Wonder Lake, Mt. McKinley National Park. At this locality spruce woods interdigitate with open tundra

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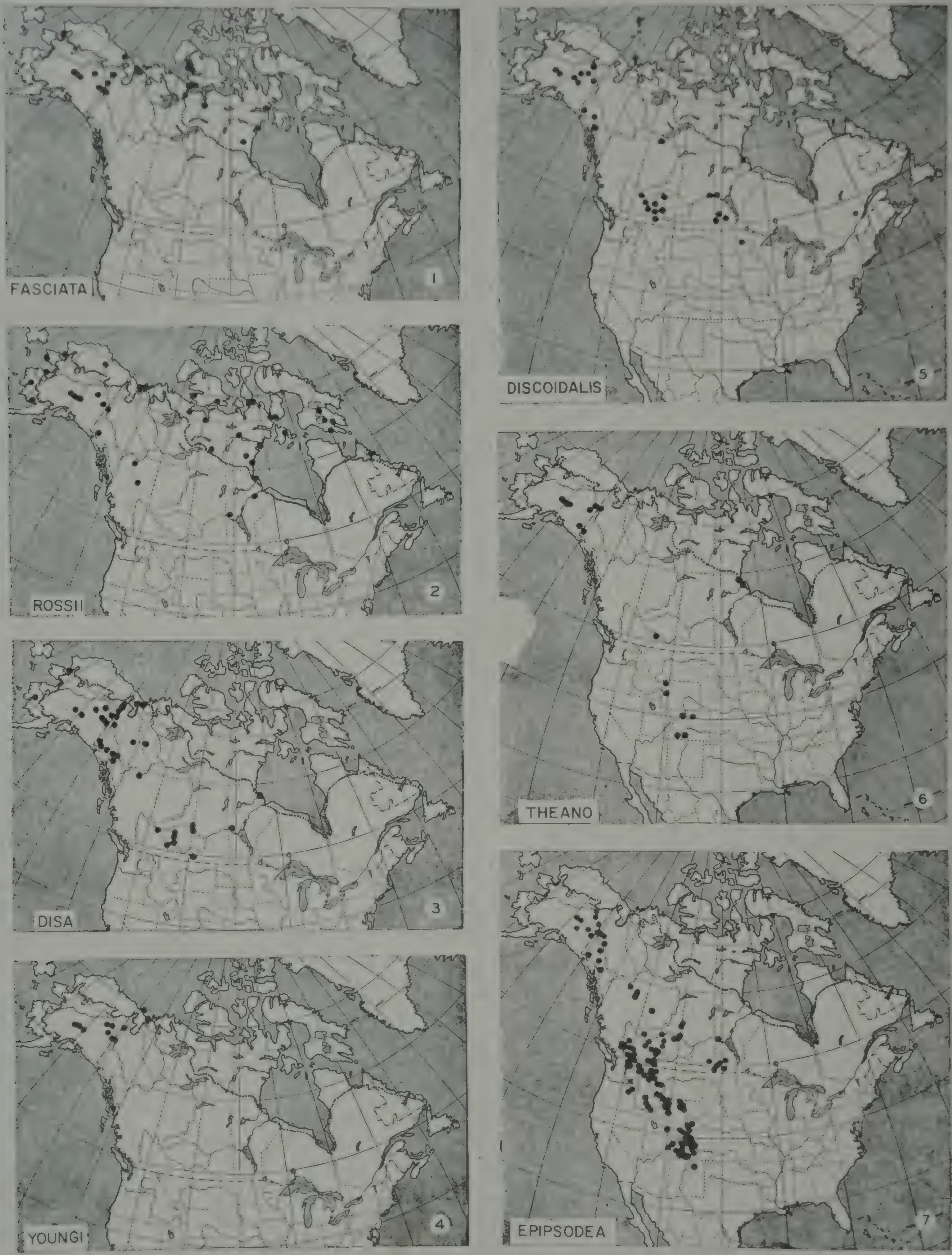

Figs. 1–7. Distributions of *Erebia* species in North America: 1, *E. fasciata* Butler; 2, *E. rossii* Curtis; 3, *E. disa* Thunberg; 4, *E. youngi* Holland; 5, *E. discoidalis* Kirby; 6, *E. theano* Tauscher; 7, *E. epipsodea* Butler.

areas at approximately 1900′. At moist spots in the road through these tundra areas *disa* was common, flying with *Erebia rossii*, *E. youngi*, and an occasional individual of *E. fasciata* or *E. discoidalis*. At roadside puddles within the spruce the other species dropped out, leaving only *disa*. In the Mackenzie Delta and Richardson Mountains, Wyatt (in litt.) reports *disa* flying with *rossii* in the tundra, and in 1956 the author found it flying in the tundra at Kotzebue, a completely treeless locality on the Chukchee Sea coast of Alaska. It was the commonest species of *Erebia*, flying in precisely the same situation as *rossii* and *fasciata*. However, as one can see from the map, *disa* is never taken far from forested areas.

Erebia discoidalis Kirby (Fig. 5) has vertical and horizontal ranges closely similar to *disa*, but flies more in open grassy areas rather than within the trees.

Erebia youngi Holland (Fig. 4) occurs north of treeline on Herschel Island, and at treeline in the Mackenzie Delta. In McKinley Park it was found principally above or at treeline, although occasionally specimens were taken in open areas along the Denali Highway within the forest. At Eagle Summit, Alaska, on the Steese Highway, *youngi* was frequent on a slope above treeline at 3500′. The slope was cut by depressions and shallow ravines which were filled with dwarf birch. Wyatt took *youngi* in the Richardson Mountains in the same type of habitat at 1200′.

In Alaska the author always found *Erebia theano* Tauscher (Fig. 6) in wooded areas, although one specimen taken at Wonder Lake was captured just at the edge of the trees. Little is known about the distribution or habits of *theano* in North America; in the United States it occurs above treeline in some areas and below in others.

Erebia epipsodea Butler (Fig. 7) occurs over a wide area in the Hudsonian, Canadian, and Upper Transition zones. The four specimens which the author took in the mountains near the Alaska-Yukon border were all well within the trees; one was taken within a few yards of an individual of *Erebia rossii.*

The accompanying diagram (Fig. 8) sums up these rather disjointed data by plotting the distribution around treeline of the *Erebia* which were taken in 1956 in the subarctic mountains of Alaska. This, of course, is a crude representation, as treeline is a very difficult parameter to estimate; one which fluctuates violently with factors such as exposure and soil type. However it does give a reference line for comparing the distributions, and unrefined as the data may be, I believe the trends are clear. Not unexpectedly the North-South and altitudinal distributions through the life zones seem well correlated.

Unfortunately, plotting *Erebia* distributions can only give clues to the basic factors causing such a diversity of patterns. How much food plant distribution affects *Erebia* ranges is not known, as life history data are almost completely lacking. All *Erebia* doubtless feed on grasses or sedges, and one would think that a suitable food supply could be found in almost any northern plant community.

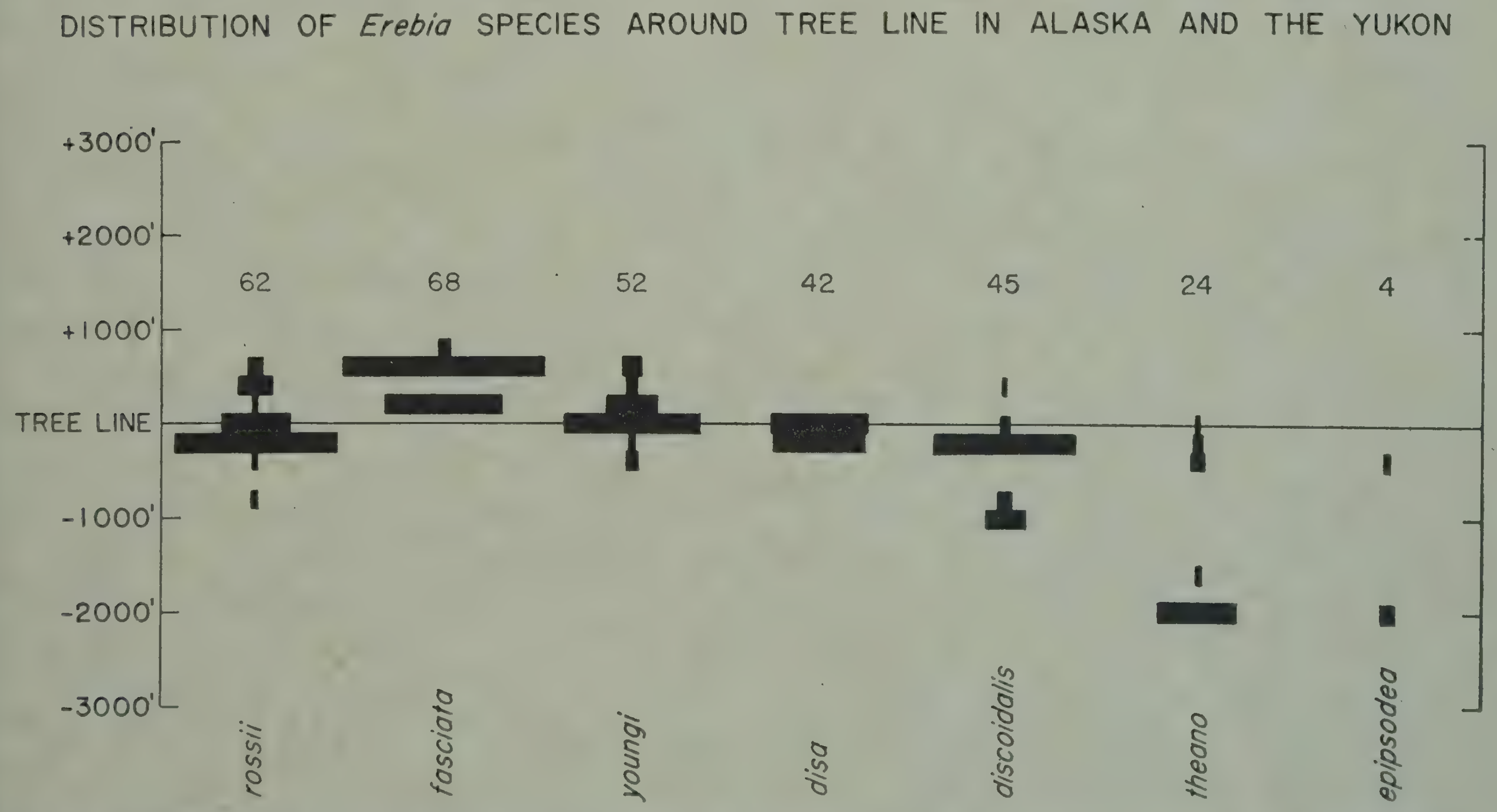

Fig. 8. Distribution of *Erebia* species around treeline in Alaska and Yukon. Numbers above each species indicate number of specimens taken.

Interspecific competition would not seem to have a large influence on *Erebia* zoogeography. The insects are single brooded, and it is difficult to imagine them building their populations in the face of such a rigorous environment to a point where individuals of the same or different species would be competing with each other for food or space. The major selective forces operating on *Erebia* populations are probably not competition, predation, or even parasitism, but rather climatic factors such as wind, cold, temperature fluctuations, snow cover, and flooding. Needless to say, field research is needed to test these informed guesses.

Both *Erebia fasciata and Erebia rossii* are probably post-glacial immigrants in North America. A factor in determining the ranges of these species may well be the amount of time which has been available to them for colonization of suitable areas. Dispersal, even for a tundra butterfly such as *Erebia fasciata*, is not a simple matter. Certainly the principal dispersing stage is the imago, which in most localities would be on the wing only two weeks out of the year. The only dispersal of significance to the species is that done by gravid females. Such females are very lethargic, flying only a few feet at a time, and usually then only if disturbed. They do not rise much above the surface of the tundra and are rarely carried by the wind. However, what of the occasional female which is picked up and carried a long distance by the wind? The chances are excellent that the individual will be carried to an unsuitable location, such as a lake or a rocky area, from which it cannot escape due to its weak flight. Should the butterfly be fortunate enough to land in an ideal location and successfully oviposit, the probability that at least a single male and female will mature can be calculated. Based on a poisson distribution and a mean survivorship of slightly more than two individuals per parental pair, and disregarding density dependent factors, the probability of such an occurrence would be of the magnitude of .40. Even if a pair is produced in such a situation, there is a considerable chance that they will not be able to mate successfully. Each succeeding generation there is some chance that the colony will be wiped out, although the probability decreases with increasing population size. Considering the multiplicative properties of independent probabilities, it can be seen that in general such leapfrog dispersal would be ineffectual. However, since colonies are doubtless occasionally established by such methods (e.g. *Erebia rossii* on Southampton and Baffin Islands etc.), we might briefly consider the genetic consequences of this type of dispersal. With each dispersing step there would be an effect similar to genetic drift. The dispersing individual would carry only a small sample from the gene pool of the parental population, and many alleles would be either lost or fixed in the new population. The resultant loss of variability in the new population could seriously hamper its ability to cope with changing situations. This effect can, of course, be counterbalanced by continuing migration from the parental population.

A problem which merits study is the effect of constant unidirectional winds on the distribution and population dynamics of tundra insects. In many areas winds during insect flight periods are almost invariably from the same direction, and this may create a situation analogous to the river model in population genetics.

In conclusion I would like to suggest that careful statistical analyses of intra- and inter-population variation based on museum material can be of great help in discovering critical areas for field work. Such tools as the analysis of variance, if applied with careful consideration of their underlying assumptions, may prove to be very informative. They are less expensive than exploratory field trips, which, considering the high cost of arctic field work, is no small advantage.

REFERENCES

Cadbury, J. W. 1938. Lepidoptera collected in northern British Columbia by Miss Josephine de N. Henry. Part I, Rhopalocera. *Proc. Acad. Nat. Sci. Philadelphia* 89: 387–413.

Ehrlich, P. R. 1956. Ecological observations on *Erebia* (Lepidoptera: Satyridae) in northwestern America. *Ent. News* 67: 29–36.

Variation in some Northern Butterflies and its Relation to Environment

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In the variation of their characters many insects show a similarity to the variation of an environmental factor. All examples I am going to adduce refer to Scandinavian butterflies.

The size of many insects varies inversely to Bergmann's rule (Petersen 1947, map 43) while the lengths of their extremities conform to Allen's rule (Alpatov 1929, Rensch 1943, Petersen 1949).

The variation of both characters is fairly well correlated with temperature of the period of growth. A similar variation applies to the time of eclosion and the number of generations per annum in e.g. *Pieris napi*.

According to the distribution of melanism there exist three types (Fig. 1):

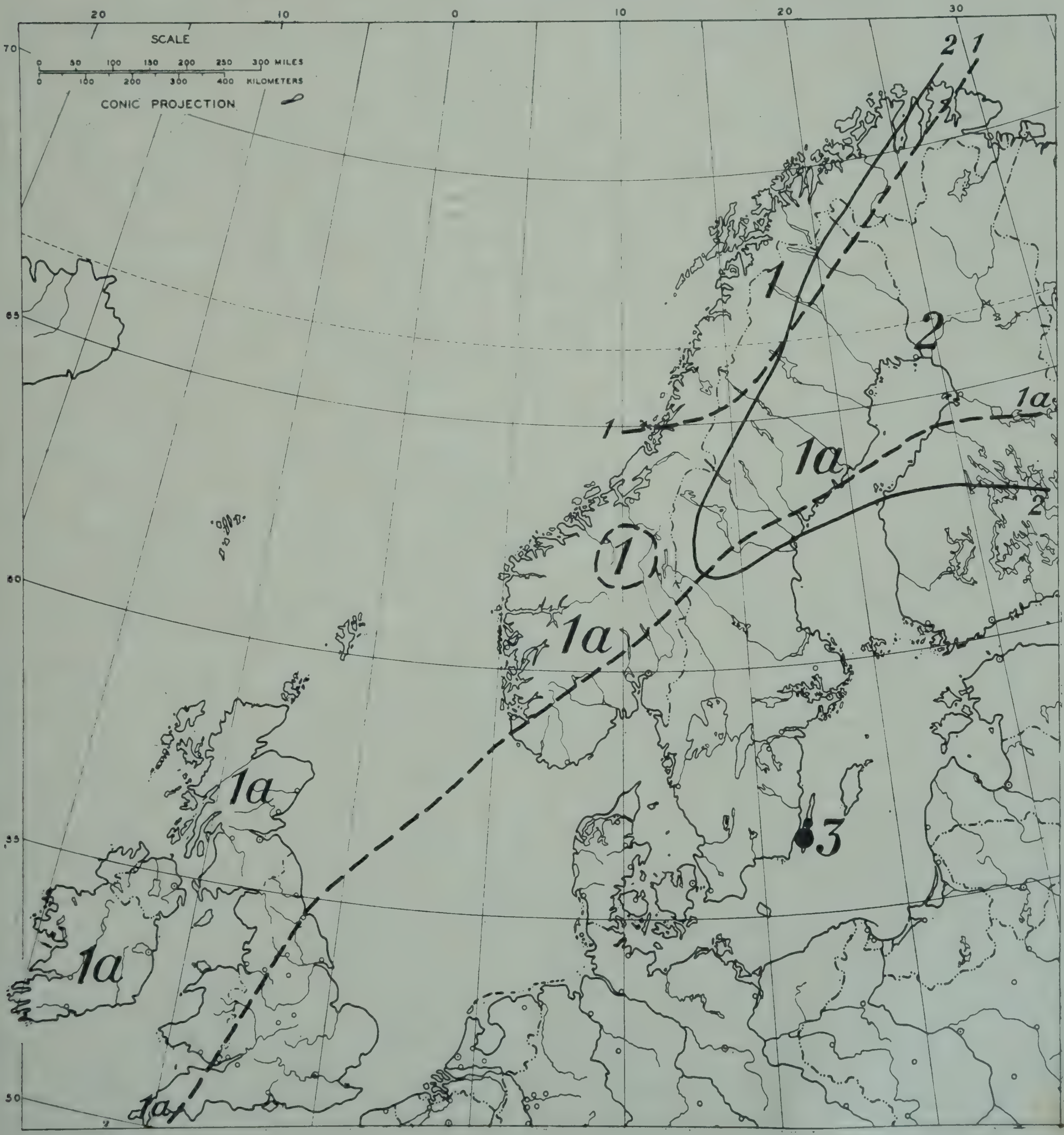
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Fig. 1. The three types of distribution of melanistic forms in Scandinavian butterflies.

1. mountain distribution (according to the distribution of *Pieris napi*), 1a. lower frequency of melanistic forms
2. northeastern distribution (*Boloria* spp.)
3. distribution of *Eumenis semele tristis*.

1. The darkest forms occur in the mountains (*P. napi*, *Erebia ligea*, *Colias palaeno*).

In a less pronounced form and with a lower frequency the dark forms may occur in adjacent areas of Scandinavia and on the British Isles (*P. napi*, area 1a of Fig. 1).

2. The darkest forms of *Boloria* spp. occur in northeastern Sweden, northern Finland, and probably further to the east.

3. Melanistic forms of *Eumenis semele* ssp. *tristis* occur on the island of Öland in the Baltic (Wahlgren 1915).

Type 1 agrees fairly well with the variation of temperature during the period of growth (Fig. 2). In *P. napi* the variation of wing colour is similar though significantly different from that of melanism. Thus at least one additional factor is involved. This factor may be habitat (food plant). *P. n. adalwinda* of the Scandinavian mountains is the only subspecies which lives in a natural habitat. It has been possible to show that the *adalwinda*-like *P.* (*napi*) *bryoniae* is in a similar way at a selective advantage in pine forests of the Alps, *P. napi* in habitats produced by man (Petersen 1955).

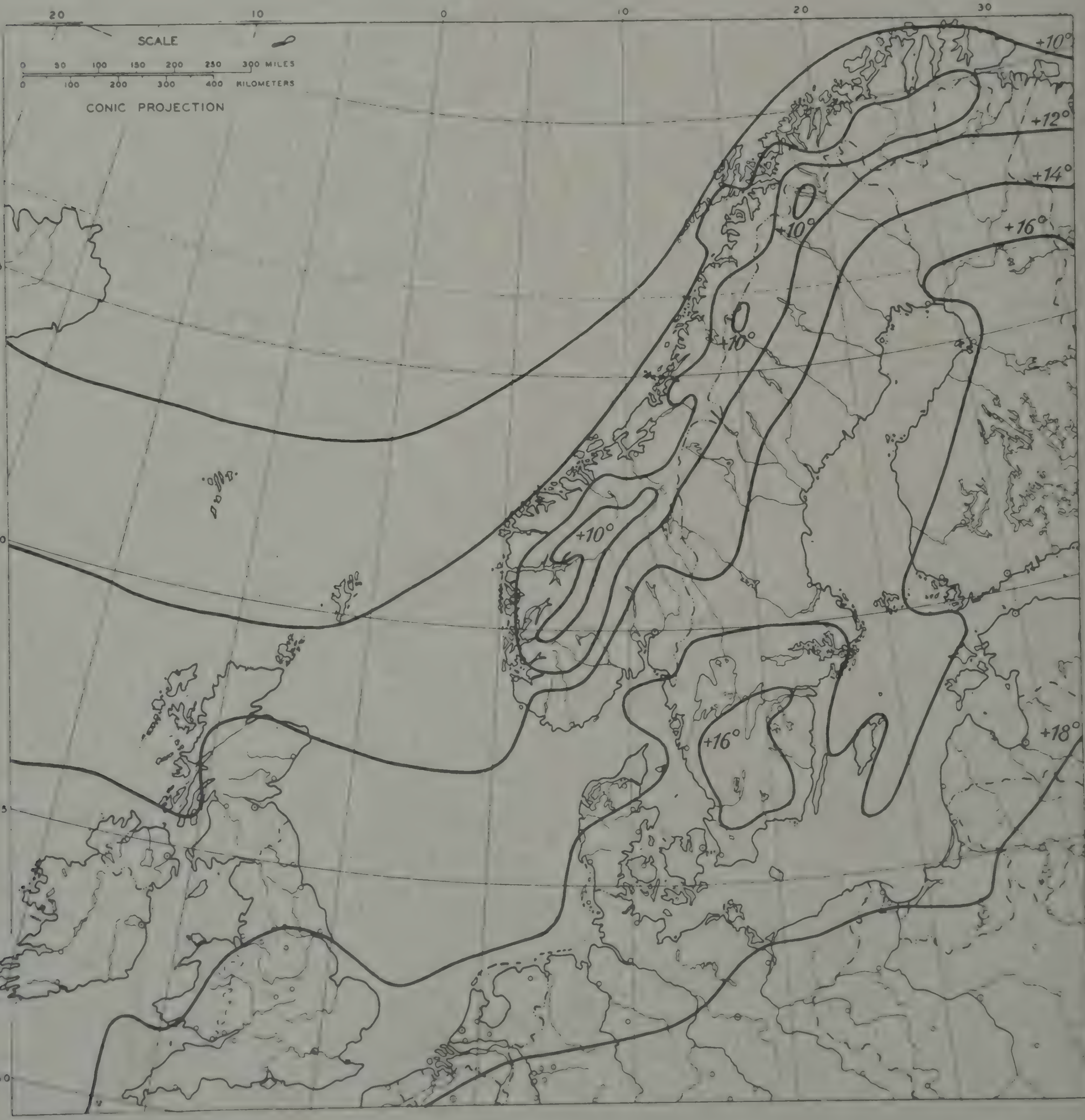

Fig. 2. The isothermes for July in northeastern Europe.

Type 2 agrees with winter temperature (Fig. 3). Whether this factor works directly or not is uncertain. The effect of the habitat is probably negligible as the variation is present in some species which are restricted to mires (*Bol. eunomia*, *frigga*).

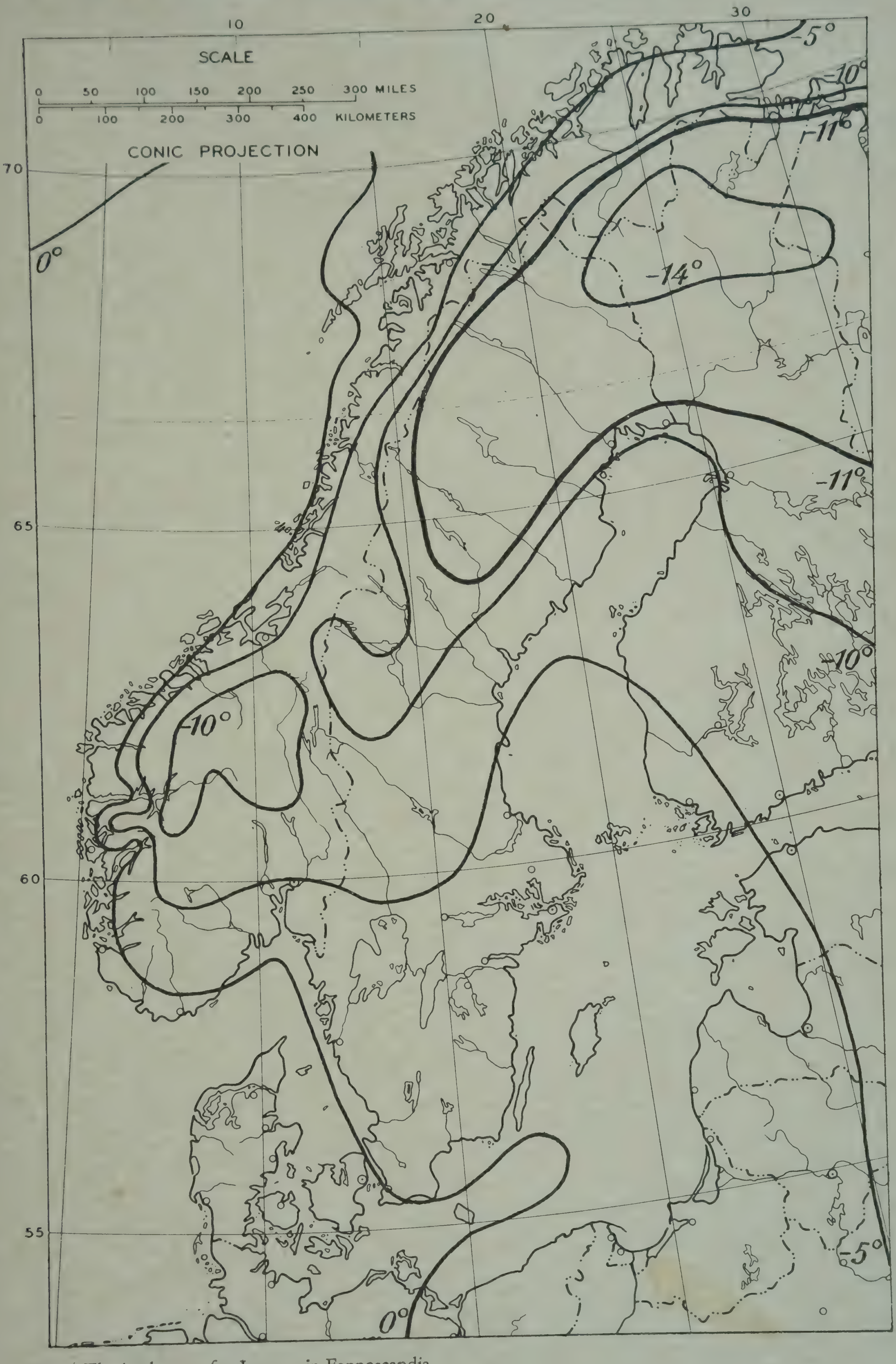
10
20
30
SCALE
0 50 100 150 200 250 300 MILES
0 100 200 300 400 KILOMETERS
CONIC PROJECTION
70
65
60
55
0°
-5°
-10°
-11°
-14°
-11°
-10°
-10°
0°
-5°

Fig. 3. The isothermes for January in Fennoscandia.

It is not possible to explain type 3 as the result of a single environmental factor. Iversen (1947) has been able to show that plants of the habitat of *E. semele tristis* are present in late glacial deposits of Denmark. The melanistic forms of type 1 and 2 are also connected with the glacial tundra. The distribution of melanistic forms in the *napi*-group is most easily explained by a dispersal during glacial times (Petersen 1954). The melanistic forms of the second type live mainly on mires. In central Europe and probably also further to the east mire species are glacial relics (Petersen 1954). Thus it is possible to explain all three types of melanism as an old tundra- (or "sub-tundra") melanism which has survived into present time in different areas.

Differentiation is a certain aspect of variation. Closely related forms of butterflies living in the mountains and on mires are different species. Most mire species are in the mountains sympatric to their mountain relatives. Lowland forms living in other habitats than mires belong to the same species as their related mountain forms. This can probably be explained by the assumption that mire forms are survivals from the Pleistocene tundra of lower latitudes. These developed relatively early during the Pleistocene, mainly from mountain forms of central Europe, central Asia, and the North-American Cordillera. Other forms which lived in a warmer climate became only later sufficiently cold-adapted as to endure the climate around the present forest limit. Due to the shorter time available the differentiation in the north has in such groups proceeded less far than in the mountain-mire-groups (Petersen 1954).

The variation within a population is in some cases dependent upon introgression. In Scandinavian *Pieris napi* the isolation between the mountain form and the lowland form has broken down almost completely. Between two similar forms of the Alps isolation is well developed in the northern part of the mountains while introgression into the mountain form is rather heavy in the south and east (Petersen 1955). Introgression was found in northern Scandinavia going from *Colias hecla* into *C. nastes* (Hovanitz and Petersen, unpublished). In the same area introgression has been found in two species groups of *Rotatoria* (Pejler 1956). Both groups occur further south but no signs of introgression have been found there. It is therefore possible that the frequency of introgression is higher in northern Europe than further south.

The variation of animals depends on many environmental factors, some of greater, others of minor importance. Here only some of the more important ones could be pointed out. For a full understanding of variation other factors such as abundance in different areas, dispersal, and all internal factors influencing variation have to be introduced into the discussion. This is, however, beyond the scope of the present paper.

REFERENCES

Alpatov, W. W. 1929. Biometrical studies on variation and races of the honey bee (*Apis mellifera* L.). *Quart. rev. biol.* 4.

Iversen, J. 1947. Plantevaekst, dyreliv og klima i det senglaciale Danmark. *Geol. Fören. Förh. Stockholm* 69: 1.

Pejler, B. 1956. Introgression in planktonic Rotatoria with some points of view on its causes and conceivable results. *Evolution* 10: 246–261.

Petersen, B. 1947. Die geographische Variation einiger fennoskandischer Lepidopteren. *Zool. bidr. Uppsala* 29.

Petersen, B. 1949. Studies on geographic variation of allometry in some European Lepidoptera. *Ibidem* 29.

Petersen, B. 1954. Some trends of speciation in the cold-adapted Holarctic fauna. *Ibidem* 30.

Petersen, B. 1955. Geographische Variation von *Pieris (napi) bryoniae* durch Bastardierung mit *Pieris napi*. *Ibidem* 30.

Rensch, B. 1943. Studien über Korrelation und klimatische Parallelität der Rassenmerkmale von Carabus-Formen. *Zool.Jb. Syst.* 76, 1942.

Wahlgren, E. 1915. Det öländska alvarets djurvärld. *Ark. zool.* 9: 19.

Ecological Studies at Churchill, Manitoba

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ABSTRACT

The various environments found at and near Churchill are described and illustrated, and discussed with regard to the situation of Churchill at timberline (the tension zone between the boreal forest and the tundra), the seral stages leading toward the forest and tundra climaxes, and the disturbances caused by man. A list of the butterflies of Churchill (at least 34 species) is given, based on past records as well as the work of the Northern Insect Survey, chiefly in 1952. A partial list of moths recorded from Churchill is also given, the moths being as yet incompletely worked up. Environment records and some new life history data for many of the species are correlated with the known data about their geographic ranges, tendencies to geographic variation and environments elsewhere.

An introductory discussion of the concept of the Hudsonian Zone is given; this is amplified in a later paper in the symposium.

Arctic Sawflies and the Open Habitat

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Some of the sawflies of the arctic tundra, and related species, occur above the tree-line on mountains as far south as the arctic tundra spread during the greatest extension of ice in the Quaternary Glacial Period, such for example as the Alps of Central Europe. They are not found on mountains beyond the reach of the maximum extent of the tundra of this period. Within this area a few, in addition, survive in isolated cliffs, screes, sandhills and marshes. But they now survive only in sites that were never overrun by forest during the Atlantic Period in Northwest Europe, or by blanket bog since.

The flora and fauna of the arctic tundra are essentially associated with open habitats and have therefore not been able to survive overshadowing by a closed community of shrubs and trees. Similar sites are also the original habitats of our ruderals, the annual weeds of recently turned-up soil. Our weeds in fact are often the same species as those that spread over the land laid bare by the retreating ice at the end of the last Glacial Period (Godwin 1949), and the same that can be seen growing today on the bare earth uncovered by melting edges of late snow patches in the Scandinavian Mountains.

On the mountains of Scotland and elsewhere in Europe where the present tree-line is considerably depressed from its maximum post-glacial level, arctic species of insects and plants are mainly to be found only well above the present line; at lower levels they are restricted to crests, screes, glacial morains, and north-facing slopes where snow patches survive late into the summer and where the snow settles first in the autumn—all sites presumably beyond the reach of the forest spread during its maximum development or of the blanket bog in more recent times; and areas that would be the first to be covered again under permanent snow on any return to glacial conditions.

In some localities in the British Isles notably on the seaboard of Southwest Ireland and the Breckland in East Anglia refugia from the forest enabled relics to survive of elements from more southern open sites, elements that had reached Britain from the Mediterranean Steppes and Iberian Peninsular.

Beirne (1952) develops a theory, unacceptable to me, for the survival of temperate elements in Britain through the last Glacial Phase on land now sunk below the sea, but he has not mentioned the more crucial problem of the survival of animals requiring open habitats through the Atlantic Forest Period.

The theory put forward by Fernald (1925), that the remarkable assortment of rare and arctic plants on Mount Albert in the Gaspe Peninsula of Quebec, had survived through the whole Glacial Period on nunataks above the ice and had not migrated since, is no longer tenable (see Rousseau 1953). For one thing the areas concerned show evident signs of having been glaciated; and for another, several of the plants have since been found to be much less restricted than was formerly thought and are now found to occur in lowland sites near the mouth of the St. Lawrence River that must have been overrun by glaciers. And Rousseau comes independently to a similar conclusion to Godwin, that such sites in Mt. Albert were refugia from the maximum forest spread, not nunataks above the ice. Nunatak theories have been put forward to explain arctic and other relics in alpine Britain and other parts of the world, but no more convincingly.

REFERENCES

Beirne, Bryan. 1952. The origin and history of the British fauna. London.

Fernald, M. L. 1925. Persistence of plants in unglaciated areas of Boreal America. *Memoirs Amer. Acad. Arts & Sci.* 15: 239–342.

Godwin, H. 1949. The spreading of the British flora, considered in relation to conditions of the Late-Glacial Period. *J. Ecol.* 37: 140–7.

Rousseau, J. 1953. The value of botany as indicator of unglaciated areas. *7th Pacific Science Congress* 5: 1–8.

Insects and Environments of the High Arctic

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ABSTRACT

The region treated in this paper is that of the Queen Elizabeth Islands of the Canadian Arctic Archipelago. These islands form a rather well-defined group that lies north of the 74th parallel and extends to 83°07′N.

The discovery and early exploration of the region are sketched very briefly. The physiography and climate are outlined and a short account of the flora and fauna is given.

Notes and observations on the insects of the region and an annotated list of the species that have been more or less reliably identified are presented.

THE AREA

There is no generally accepted definition for the term "high arctic". Therefore, the area treated in this paper has been rather arbitrarily restricted to the northernmost group of islands of the Canadian Arctic Archipelago that are now known as the Queen Elizabeth Islands. This group forms a well-defined geographical unit that is separated from the remainder of the archipelago by a broad water-way consisting of Lancaster Sound, Barrow Strait, Viscount Melville Sound, and McClure Strait.

The Queen Elizabeth Islands lie entirely north of the 74th parallel and extend at Cape Aldrich to 83°07′N., that is to within 470 miles (750 km.) of the North Pole. They include thus some of the northernmost lands of the globe.

The shape of the area is roughly triangular, with the base running east-west for a distance of 725 miles (1016 km.). The distance from base to apex is about 625 miles (1000 km.), and the area, in round figures, 200,000 square miles (518,000 km.^{2}). The area of land is about equal to that of Great Britain, 165,000 square miles (430,000 km.^{2}).

HISTORY

The first Europeans to visit the area may have been Norsemen from Greenland in the eleventh to the thirteenth century. The slim evidence for this is controversial and the first documented landing on any of the islands was made during the voyage of the 55-ton *Discovery* under Bylot and Baffin in 1616. Baffin's report was disregarded and forgotten until John Ross in 1818 confirmed it. Parry discovered the southern islands as far west as Melville Island in 1819–20. They were explored in greater detail and the discoveries extended to Prince Patrick Island during the prolonged search for the lost Franklin Expedition around the middle of the 19th century.

The eastern boundary of the area was discovered and explored during the second half of the 19th century by Inglefield, Kane, Hayes, and Hall. The British Arctic Expedition under Sir George Nares in 1875–6 extended the exploration to the north and northwest coasts of Ellesmere Island and its members made the first important contributions to the botany and entomology of the region. The ill-starred United States Arctic Expedition under Lt. Greely on the occasion of the First International Polar Year in 1881–4, explored some of the interior of northern Ellesmere Island.

The Second Norwegian Arctic Expedition in the "Fram", 1898–1902, under Otto Sverdrup added greatly to our knowledge of the geography of the central and northwestern parts of the islands and made valuable additions in the field of natural history. The last gaps along the northwest boundary were filled by Stefansson during the Canadian Arctic Expedition of 1913–18.

Since that time a number of expeditions have visited the area for various purposes, but no contributions to entomology worth mentioning were made.

GEOLOGY AND TOPOGRAPHY

The geology of the Queen Elizabeth Islands is at present known only in broad outline. Precambrian rocks of the Canadian shield are restricted to marginal outliers in eastern Devon Island, in south-eastern and eastern Ellesmere Island and to a small, detached area in northern Ellesmere Island.

Two wide belts of folded palaeozoic strata cross the whole group. The first occupies most of the southern islands, from Melville Island to Wellington Channel; the other stretches from western Devon Island across the centre of the southern half of Ellesmere Island to the northeastern part of it. To the west and northwest of the folded belts occur flat lying to gently dipping strata of mostly softer rocks of mesozoic age.

The areas of greatest relief lie in the eastern part, where elevations of up to 10,000 feet (3,000 m.) are reported from northern Ellesmere Island and central Axel Heiberg Island. The other islands are much lower, seldom over 1,000 feet (300 m.), amd mostly not much over 500 feet (150 m.) high. Only a few mountains in western Melville Island attain 3,000 feet (900 m.).

Glaciers, local ice caps, and permanent snowfields of often considerable size are confined to the high lands in the east, that is, Meighen, Axel Heiberg, Ellesmere, and parts of Devon islands. The western and northwestern islands are blocked by sea ice all year round; but Melville Island, Eureka Sound, and Alert can be reached by icebreaker in practically every summer.

CLIMATE

The joint United States-Canadian arctic weather stations at Resolute, Cornwallis Island; Eureka, Ellesmere Island; Mould Bay, Prince Patrick Island; Isachsen, Ellef Ringnes Island; and Alert, Ellesmere Island, were established between 1947 and 1950. They have provided reliable information on the climate of our region. Since all these stations are coastal, it is not surprising that they have, with the exception of Eureka, a modified maritime climate with short, cool, cloudy, and rather windy summers, and long, comparatively clear, calm, but not very severe winters. Eureka, where the adjoining water-masses are small and which is sheltered from the direct influence of the Arctic Ocean by Axel Heiberg Island, has a more continental type of climate. The Eureka records indicate the type of climate that probably prevails in the interior of the larger islands.

The mean temperature for the year lies around 0°F. (−18°C.). During the winter, when the sun is continuously below the horizon from November to February, the average monthly means lie in the range of −30° to −40°F. (−34° to −40°C.). In May they reach the freezing point and remain above it for at least two months (at Alert, Isachsen, and Mould Bay), or three months (at Eureka, Craig Harbour). The sun remains above the horizon from April to the end of August, and during the short arctic summer the weather can be very pleasant. The average mean temperature for July, the warmest month, varies between 37°F. (2.8°C.) at Mould Bay and 41°F. (5°C.) at Eureka. Even during this month frost occurs regularly at all stations, except at Eureka. The recorded extremes of temperature are −65°F. (−54°C.) at Isachsen and +67°F. (+19.4°C.) at Eureka.

Precipitation is very light. The yearly total varies from 3 inches in the northwest to 10 inches in the southeast; but Eureka has an 8-year average of only 2.44 inches. About one-third of the total falls as rain; but the proportion can be as small as one-eighth at Alert and as large as seven-eighths at Eureka. Falls of snow, sufficient to make the ground white, occur in every month, even in July; however, at that time of year the snow persists for only a few hours, except at higher elevations.

It can safely be said that the climate in general becomes severer and less pleasant the farther one travels from southeast to northwest. Features of the flora and insect fauna reflect this very clearly.

FLORA AND FAUNA

From the earliest times on, arctic explorers have brought home collections of plants that contained at least the more showy and common species. Although no professional botanist has spent more than a few hours or days at any place in the Queen Elizabeth Islands, except at Resolute and the south coast of Ellesmere Island, the flora of the region is fairly well known to-day.

Of the 327 species of vascular plants that are recorded for the entire Canadian Arctic Archipelago, 156 have been found in our area. At least 148 of these occur in Devon, Ellesmere, and Axel Heiberg islands, but from the remainder of the region only 106 are known. For the whole of Ellesmere Island 143 species have been recorded; 65 of these have been collected at Alert and 100 at Eureka. At this locality one species, *Geum rossii* (R.Br.) Ser., was found that occurs elsewhere in our area only in Melville Island, the type locality, where it was collected in 1820, and in Axel Heiberg Island. It is common in the Yukon, parts of Alaska and eastern Asia. Related species occur at high altitudes in the Cordillera as far south as New Mexico. Incidentally, among the plants of one collection of *Geum* I found the only beetle seen in the high Arctic, a member of the genus *Atheta*.

One of the most widely distributed arctic plants is the purple saxifrage, *Saxifraga oppositifolia*. It is the true harbinger of spring and later covers whole hillsides with a purple sheen. It was nowhere more splendid than at Alert. Equally common is *Salix arctica*. Its branches hug the ground closely and send up catkins that look like pink candles. The arctic poppy, *Papaver radicatum*, is yellow-flowered in the southern part of the area and at low elevations. In the north and on the mountains about one-half of its blossoms are white. It also showed its best development at Alert. Some very showy flowers, as *Erysimum pallasii*, grow only in the most desolate and inhospitable places. Few arctic flowers are scented. Outstanding among the exceptions is *Astragalus alpinus*, the arctic milk-vetch, which is a great attraction to bumble bees at Mould Bay. It belongs to the Leguminosae, a family that is entirely lacking in Ellesmere Island. There its place as insect favourite is taken by several showy species of lousewort, *Pedicularis*.

Among the mammals pride of place belongs to the monarch of the Arctic, the musk ox, *Ovibos moschatus*. It is widely distributed in the islands and, thanks to strict protection, appears to maintain its numbers well. The Peary caribou, *Rangifer pearyi*, is not as numerous, nor as generally distributed. The arctic hare, *Lepus articus*, which stays white all year, has the curious habit of travelling at great speed erect on its hind legs when alarmed. Along Eureka Sound it has been observed in flocks numbering over 500 animals. The collared lemming, *Dicrostonyx groenlandicus*, furnishes one of the classic examples of great periodic fluctuations in abundance. Among the predators, the first that comes to mind, when thinking of the Arctic, is most likely the polar bear, *Thalarctos maritimus*. It is very rare in the west and north of the area, and there the only signs of its presence were ancient tracks. Arctic wolves, *Canis lupus arctos*, which do not change colour seasonally, are great wanderers. They are occasionally met in packs numbering up to ten or rarely more animals, but they are cowardly and harmless to man. Apparently they do not find their tables well decked, most of those shot were very thin. The arctic fox, *Alopex lagopus*, a very graceful animal that becomes tame quickly and that will take bits of bacon or cheese very gently from one's hand, turns brown in the summer and has at times a most ludicrous aspect. The smallest of the carnivores, the weasel, *Mustela erminea*, also changes colour. It is rather rare in the far north, but probably strays to the northernmost parts of Ellesmere Island.

Among the birds are a number of waterfowl, including the snow goose, *Chen hyperborea*, which breeds as far north as Alert; several species of shore birds, among them knot, *Calidris canutus*, and turnstone, *Arenaria interpres*. Raven, *Corvus corax*, and snowy owl, *Nyctea scandiaca* are rare when lemmings are scarce. Gyrfalcons, *Falco rusticolus*, and ptarmigan, *Lagopus mutus*, decline in numbers toward the north. The cheerful little song of the snowbunting, *Plectrophenax nivalis*, can be heard everywhere from May till September, no matter how foul the weather.

INSECTS

In contrast to botany, entomology had been sadly neglected by arctic explorers in general and in particular by the early visitors to our region. Prior to the Nares expedition only the officers on Parry's first voyage in 1819–20 brought back a few insects that were reported on by Kirby (1824). Even now, no professional entomologist has spent more than a few hours or days in any part of the Queen Elizabeth Islands. I myself cannot lay claim to be anything more than a lepidopterist. It is, therefore, hardly astonishing that my list of species for the region contains only 93 names of insects proper. These are divided among ten orders, of which the Diptera are best represented with 28 species, followed by the Hymenoptera with 23, and the Lepidoptera with 18.

In the following lines I shall give a few remarks, random notes, and observations, which may be of some interest. The botanist who goes to a place in the Arctic may hope to find at least all those species of plants that have been recorded for that locality; but he soon finds that he needs a certain amount of luck to realize his ambition. Plants, especially those that grew near the limit of their distribution, often occur only in very small stands, more often than not tucked away in a hidden or inaccessible spot. Unless he stumbles on it, he will miss that species.

How close one can come to overlooking a species, I learned at Alert, where I stopped and rested several times within 100 yards of a large stand of the assiduously sought-for and quite conspicuous *Epilobium latifolium* without seeing it, because only on the last visit did I climb to the topmost of three gravel terraces, where alone it grew in profusion.

The entomologist faces even greater difficulties. He must not only find the right spot, he must also find it or visit it at the right moment. How fleeting this moment can be, my experience with the large, brightly coloured syrphid *Helophila borealis* will show. In July 1953 I was travelling with a 60-lb. pack to establish a camp at Eastwind Lake. In bright sunshine I stopped at the marshy edge of a pond to have a look at a family of snow geese, when I noticed the syrphids over the water. Before I had stepped back to dry ground, dropped the pack and returned to the pond, the edge of a heavy overcast had obscured the sun and the insects had disappeared. Twice I revisited the pond to collect the flies and photograph the geese and twice it had started to rain when I reached it. If I had not been able to return to Eureka the following year and found a more favourable season, I should not have known what species I had seen.

Sometimes a specimen appears like a bolt out of the blue, like my first *Syngrapha parilis* that settled at my feet when I was resting at one of the few well vegetated spots along the coast of Slidre Fiord on the afternoon of August 28, 1953, during a spell of a few hours of real "Indian summer". No insects whatever had been on the wing for a fortnight and I had given up carrying a net! Fortunately, I managed to clamp my beret over the moth and secure it. In the following year a series of 12 was collected without much effort.

How quickly the weather can change is shown by the fact that only ten hours later, at 0200 hrs. the next morning, I was facing a snowstorm that left the ground white. But the collector has not only to contend with the vagaries of the weather. The habits of his prey are often disconcerting and may become serious obstacles to his success. Sweeping, for instance, does not work at all in the high Arctic. For one thing, the vegetation is sparse and so low that it is practically impossible to avoid picking up dirt and gravel. The main reason for the failure of this method is the fact that the insects will not fly up, or even stay on the wing; they simply drop down among the litter. There it is difficult to pick them up even with an aspirator or with foreceps. When collecting flies around a rotting musk ox skull, the calliphorids could be netted, but the scatophaga had to be picked up one by one with aspirator or foreceps.

By far the most common caterpillars are those of *Byrdia groenlandica*. They can be collected by the score, but the moths are seldom seen and still more rarely taken, especially the males. They fly high, fast and erratically, and can be captured only accidentally, as the one that landed obligingly in the—fortunately empty and dry—cup of a thermos bottle. The females apparently do not fly at all. One was found that had deposited all its eggs on the cocoon from which it had emerged. It is difficult to find sound cocoons; most of those that are not too well hidden have been robbed by long-tailed jaegers or turnstones.

With caterpillars, at least those of *Byrdia*, in such good supply, it may be thought that it would be easy to rear large numbers in the laboratory. Unfortunately, this is by no means so. Disregarding the fact that a very high percentage—probably 50 to 75 per cent—are parasitized, they take several years—three or four at least—to mature. Unless the collected larva is about ready to pupate, it will feed for only a very limited period, usually not much longer than two weeks, even under favourable temperature and light conditions, spin up and go into aestivation, which leads directly into hibernation.

Attempts to rear larvae in the insectary at Ottawa have failed. Pupae of *Byrdia* appear to be indestructible. A few that had been misplaced in packing in 1953 were frozen and thawed several times in transit. They were then stored in a dry room at temperatures between 70° and 80°F. (22° to 27°C.); in the spring of 1954 they were shipped back to Eureka, and, after being frozen and thawed at least once more, yielded one male and two females.

Among the numerous larvae of *Byrdia groenlandica* collected at Eureka were odd ones—about four specimens in each season—that differed considerably in colour and arrangement of hair pencils from the general run. Attempts to rear these failed entirely, which was the more disappointing as I had cherished the hope that they might be arctiid caterpillars. Later on Miss MacKay kindly examined two of these larvae and found that they fitted exactly the descriptions of those of *Byrdia rossii*, which is of a much more southerly distribution than *B. groenlandica*.

The first insects to appear on the wing are midges and blowflies—the former are also the last to disappear when winter approaches. Bumble bees are not far behind and come out as soon as the first flowers open. Their heavy bodies, clothed with long, dense hair adapt them to fly under adverse weather conditions, as the following observations show. At Alert on the afternoon of August 3 everything was coated with hoarfrost. At 2000 hrs., with the sun shining and a light breeze blowing, the air temperature was 25.5°F. (−3.6°C.), a thermometer lying on the ground on a north-facing slope registered 38°F. (3.3°C.). At the same time several *Bombus* were flying in and out of their nest. On July 23 at Mould Bay the ground was white with snow and the air temperature varied between 29° and 34°F. (−1.7° and +1.1°C.). At 0700 hrs. a bumble bee was trying in vain to gain enough altitude to clear the roof of a building. It finally flew around the end of the building, making no sound whatever.

Mosquitoes do not fly as long as the air temperature is below 45°F. (7.2°C.). *Aedes impiger* Wlk., better known as *nearcticus* Dyar, was quite common at Alert around the middle of July. To me its bite is painless and harmless, but in one of the strip mechanics its bites had caused an inflammation of the back of the neck. At Eureka *A. nigripes* (Zett.) occurred together with *impiger* in numbers in 1953. Both species were very abundant in 1954 and apparently also in 1955. The bite of *nigripes* is quite painful and I had to use repellent almost continuously from the last week of June to the first part of August. In 1954 they were obviously molesting the musk oxen that were very restless, much more so than during the previous season. Plain evidence that the mosquitoes were bothering small mammals was provided by the behaviour of a half-grown arctic hare. The little fellow attracted my attention by its queer antics while I was breaking camp at Eastwind Lake. It came rushing into camp, stopped, made a complete turn with all four feet off the ground, waved its long ears like flails, tried to hide underneath some camp gear and between my feet. In the end I noticed a mosquito settle on the tip of one ear, which triggered another pirouette.

McLachlan (1879) cites as the most northerly locality for the *Boloria* taken by Capt. Feilden the latitude 81°52′N. This is half a degree south of Floeberg Beach, the wintering place of the *Alert*. I collected ten specimens of *Boloria chariclea* and *polaris*, all of them north of Floeberg Beach. Hattersley-Smith collected *chariclea* at Disraeli Bay, at almost 83°N. 40 miles west of Cape Aldrich, the northernmost tip of Ellesmere Island. Does the failure of Feilden to collect *Boloria* north of 81°52′N. mean that the butterfly has spread since 1876 that much farther north and west, because the climate has ameliorated? Or was the summer of 1876 so unfavourable that the butterflies did not emerge? The scant weather data available for the Nares Expedition do not make it possible to answer the last question.

In 1953 at Eureka, the butterflies and most of the moths seemed to be concentrated in certain favourable spots. This made it possible to collect almost 150 specimens in one afternoon during a few hours. In the following year no such concentrations were observed, but Lepidoptera and other insects were more common than in the previous season and were encountered almost everywhere. One of the Eureka captures perhaps deserves mentioning. That is *Stenoptilia mengeli* Fern. of which one specimen was taken in 1953 and two more at almost the same spot in 1954. This is 2.5 degrees north of the type locality in West-Greenland. Equally remarkable is the capture of a long series of caddisflies of the genus *Radema* at Alert. The only other locality in the Queen Elizabeth Island where caddisflies have been collected is Resolute.

The establishment of the joint arctic weather stations has made it possible to carry out scientific work in the high Arctic in relative comfort. But that does not mean that the entomologist can do his collecting without hard work. Except at Mould Bay, the immediate surroundings of the weather stations are the poorest collecting grounds. As there is usually no transport of any kind available for the visitor, a great deal of walking is necessary. Since there are no roads or trails, most of the walking is over indifferent or even bad footing.

I wish to acknowledge a great debt of gratitude to the United States Army Air Force and the Royal Canadian Air Force for transportation over many thousands of air miles; to the United States Weather-Bureau and the Metereological Division of the Canada Department of Transport for their hospitality at the stations; to the personnel of the weather stations for their many kindnesses and never-failing help. Furthermore to the officers of the Canadian Wildlife Service, who helped to make a second season at Eureka possible, who arranged helicopter flights, and the loan of a Packtractor from the Canadian Army.

I am most grateful to Dr. T. N. Freeman, Co-ordinator of the Northern Insect Survey, Mr. G. P. Holland and other officers of the Entomology Division, Canada Department of Agriculture, without whose kind help and support it would not have been possible to achieve, at the last minute so to say, the realization of a life-long ambition: to collect in the high Arctic.

LIST OF INSECTS RECORDED FROM THE QUEEN ELIZABETH ISLANDS

Abbreviations:

Nares = British Arctic Expedition, 1875–76, under the command of Captain Sir Georges Nares.

Fram = Second Norwegian Polar Expedition in the *Fram*, 1898–1902.

Parry = Voyage for the discovery of a North-West Passage from the Atlantic to the Pacific; performed in the years 1819–20, etc.

NIS = Northern Insect Survey. Records other than those of the author have collector's name in [ ].

CNC = Specimens in the Canadian National Collection, Ottawa; name of collector in [ ].

Lepidoptera

Colias hecla Lef.—Nares: Discovery Harbour, Hayes Sound.
Fram: Fort Juliane.
NIS: Eureka.
Boloria chariclea Schneid.—Nares: Shiftrudder Bay, Discovery Harbour, Hayes Sound.
Fram: Harbour Fiord.
NIS: Alert, Eureka.
CNC: Disraeli Bay [Hattersley-Smith], Craig Harbour [?].
B. polaris Bdv.—Nares: Shiftrudder Bay, Discovery Harbour.
Fram: Rice Strait, Harbour Fiord, Goose Fiord.
NIS: Alert, Eureka.
Lycaena phlaeas feildeni McLach.—Nares: Discovery Harbour.
Plebeius aquilo Bdv.—Nares: Discovery Harbour.
Fram: Fort Juliane, Harbour Fiord.
CNC: Craig Harbour [?].
Lasiestra leucocycla Staud.—Fram: Rice Strait, Harbour Fiord.
Anarta richardsoni Curt.—Nares: Dobbin Bay.
Fram: Rice Strait, Harbour Fiord, Goose Fiord.
NIS: Alert?, Eureka.
CNC: Eureka (ex *Stercorarius longicaudus*) [MacDonald & Parmelee].
Crymodes nr. *exulis* Lef.—CNC: Eureka (ex *Stercorarius longicaudus*) [MacDonald & Parmelee].
Syngrapha parilis Hbn.—Nares: Hayes Sound.
NIS: Eureka.
CNC: Eureka (ex *Stercorarius longicaudus*) [MacDonald & Parmelee)].
Byrdia groenlandica Hom.—Nares: Cape Joseph Henry, Alert to Hayes Sound.
Fram: Goose Fiord.
NIS: Alert, Eureka, Mould Bay (larva only), Resolute?
CNC: Ward Hunt Island, Disraeli Bay (larvae only) [Hattersley-Smith].
B. rossii Curt.—NIS: Eureka (larvae only).
Dasyuris polata Dup.—Fram: Rice Strait.
NIS: Eureka.
CNC: Craig Harbour [?].
Psychophora sabini Kby.—Parry: Winter Harbour, Melville Island.
Nares: Alert, Shiftrudder Bay, Discovery Harbour.
Fram: Cape Rutherford, Muskox Fiord, Harbour Fiord, Hell Gate. Goose Fiord.
NIS: Alert, Eureka, Mould Bay; Resolute [Smith & Butler].
CNC: Ward Hunt Island, Disraeli Bay [Hattersley-Smith]; Isachsen [Heywood]; Craig-Harbour [?].
Udea torvalis Möschl.—Nares: Alert, Discovery Harbour.
Fram: Harbour Fiord, Goose Fiord.
Stenoptilia mengeli Fern.—NIS: Eureka.

Olethreutes inquietana Walk.—Fram: Harbour Fiord.
NIS: Alert?, Eureka.
O. mengelana Fern.—Fram: Cape Rutherford, Rice Strait, Harbour Fiord, Goose Fiord.
Olethreutes sp.—Nares: Alert, Discovery Harbour.

COLEOPTERA

Atheta sp.—NIS: Eureka.
Lathridius minutus L.—Fram: Alexandra Fiord.
Micralymma brevilingue Schiödte—Fram: Cocked Hat Island.
Quedius fulgidus Erichson—Nares: Discovery Harbour.

HYMENOPTERA

Nematus borealis Marlatt—Fram: Goose Fiord.
N. stordalensis Strand—Fram: Harbour Fiord, Big Valley.
N. marginifer Strand—Fram: Breitstad Fiord.
Nematus sp.—CNC: Eureka (ex *Stercorarius longicaudus*) [MacDonald & Parmelee].
NIS: Mould Bay (same sp.?).
Pachynematus sp.—CNC: Ward Hunt Island [Hattersley-Smith].
Ichneumon erythromelas McLach.—Nares: Alert.
Fram: Rice Strait?.
I. amauropus Heinrich—CNC: Alert [?].
Ichneumon sp.—NIS: Eureka; Resolute [Smith & Butler].
Cryptus arcticus Schiödte—Nares: Rawlings Bay.
NIS: Eureka.
Opidnus sp.—NIS: Eureka.
Atractodes sp.—NIS: Resolute [Smith & Butler].
Eriplanus sp.—NIS: Eureka.
Phygadeuon sp.—NIS: Eureka.
Apanteles n. sp. nr. *alticola*—NIS: Alert.
Apanteles n. sp. B.—NIS: Eureka.
Apanteles sp. (= *Microgaster*)—Nares: Dobbin Bay. (? = A. *hallii* Pack.).
Rogas sp.—NIS: Eureka.
Campoletis sp.—NIS: Eureka.
Hyposotor luctus Ds.—NIS: Alert, Eureka.
Bombus arcticus Kby.—Parry: Winter Harbour, Melville Island.
Nares: Discovery Harbour, Hayes Sound.
Fram: Cape Rutherford, Fort Juliane, Rice Strait, Harbour Fiord, Goose Fiord.
NIS: Alert, Eureka, Mould Bay.
B. hyperboreus Schönh.—Fram: Rice Strait, Harbour Fiord, Goose Fiord.
NIS: Alert, Eureka, Mould Bay.

DIPTERA

CULICIDAE

Aedes impiger (Walk.) (= *nearcticus* Dyar) — NIS: Alert, Eureka.
A. nigripes (Zett.)—Nares: Hayes Sound.
NIS: Eureka.
Aedes hexodontus Dyar—NIS: Mould Bay.

SCIARIDAE

Sciara sp.—Nares: Alert.
Sciara sp.—NIS: Mould Bay.

CHIRONOMIDAE

Chironomus polaris Kby.—Parry: Winter Harbour, Melville Island.
Nares: Alert.
Orthocladius sp.—CNC: Ward Hunt Island [Hattersley-Smith].
Protanypus sp.—CNC: Ward Hunt Island [Hattersley-Smith].
. . . . . . NIS: undetermined numbers of genera and species have been collected Alert, Eureka, and Mould Bay.

TIPULIDAE

Dactylolabia rhicnoptiloides (Alex.)—Fram: Harbour Fiord.
NIS: Eureka, Mould Bay; Resolute [Smith & Butler].
CNC: Eureka (ex *Stercorarius longicaudus*) [MacDonald & Parmelee].
Tipula arctica Curt.—Parry: Winter Harbour, Melville Island.
Nares: no localities given.
Fram: Rice Strait, Cape Rutherford, Harbour Fiord, Goose Fiord.
NIS: Alert, Eureka, Mould Bay; Resolute [Smith & Butler].
CNC: Eureka (ex *Stercorarius longicaudus*, larvae ex *Calidris canutus* and ?*Plectrophenax nivalis*) [MacDonald & Parmelee].

EMPIDIDAE

Rhamphomyia ursinella Mel.—NIS: Mould Bay.

SYRPHIDAE

Helophilus borealis Staeger—NIS: Eureka.
Metasyrphus chillcotti Fluke—NIS: Eureka.
Stenosyrphus bulbosus Fluke—NIS: Eureka.
Melanostoma sp.—NIS: Eureka.
CNC: Ward Hunt Island [Hattersley-Smith].

Epistrophe sp.—NIS: Alert?
CNC: Ward Hunt Island [Hattersley-Smith].
TACHINIDAE
?Genus, 2 spp.?—Nares: no localities.
Exorista n. sp.—NIS: Alert, Eureka; Resolute [Smith & Butler].
Genus nr. *Trafoia* B. & B.—NIS: Mould Bay.
CALLIPHORIDAE
Boreellus atriceps (Zett.)—NIS: Alert, Eureka, Mould Bay.
CNC: Ward Hunt Island [Hattersley-Smith], Craig Harbour [?].
Protophormia terranovae (R.D.)—NIS: Alert, Eureka.
CNC: Craig Harbour [?].
SCATOPHAGIDAE
Scatophaga apicalis Curt.—NIS: Alert, Eureka.
S. nigripalpis Beck—NIS: Eureka.
S. multisetosa (Holmgren)—NIS: Eureka.
EPHYDRIDAE
Lamproscatella n. sp.—NIS: Eureka.
MYCETOPHILIDAE
Exechia sp.—NIS: Alert.
Exechia sp.—NIS: Resolute [Smith & Butler].

The following, reported by Osten-Sacken from the Nares Expedition, are not arctic species and cannot be placed with certainty: *Trichocera regelationis* L., *Pyrellia cadaverina* Kby., *Anthomyia* sp.

HEMIPTERA

Hematopinus trichechi Boheman—Nares: Walrus Island.

ORTHOPTERA

Blatella germanica L.—NIS: Alert (introduced in 1951, became pest in 1952).

TRICHOPTERA

Radema sp.—NIS: Alert, Resolute? [Smith & Butler].

SIPHONAPTERA

Haplopsyllus glacialis glacialis (Taschenb.)—NIS: Eureka (ex *Lepus arcticus*).

MALLOPHAGA

Nares: 7 species. Fram: none recorded. NIS: none determined.

COLLEMBOLA

Nares: 3 species. Fram: 6 species. NIS: none determined.

LIST OF LOCALITIES

Alert 82°30′N, 62°20′W; Alexandra Fiord 78°50′N, 76°20′W; Big Valley 76°28′N, 84°20′W; Breistad Fiord 79°02′N, 78°15′W; Cape Joseph Henry 82°42′N, 63°30′W; Cape Rutherford 78°49′N, 75°00′W; Cocked Hat Island 78°48′N, 74°50′W; Craig Harbour 76°12′N, 79°35′W; Discovery Harbour 81°43′N, 64°45′W; Disraeli Bay 82°55′N, 75°00′W; Dobbin Bay 79°48′N, 74°00′W; Eureka 80°00′N, 85°56′W; Fort Juliane 79°03′N, 77°00′W; Goose Fiord 76°45′N, 88°38′W; Harbour Fiord 76°29′N, 84°04′W; Hayes Sound, around 79°N, 77°W; Hell Gate 76°35′N, 89°20′W; Isachsen 78°47′N, 103°32′W; Mould Bay 76°16′N, 119°50′W; Muskox Fiord 76°30′N, 87°30′W; Rawlings Bay 80°20′N, 70°00′W; Resolute 74°41′N, 94°54′W; Rice Strait 78°45′N, 74°56′W; Shiftrudder Bay 81°50′N, 63°30′W; Walrus Island 79°23′N, 74°30′W; Ward Hunt Island 83°05′N, 74°30′W; Winter Harbour, Melville Island 74°47′N, 110°58′W.

REFERENCES

Alexander, Ch. P. 1924. Report of the second Norwegian expedition in the *Fram*, 1898–1902. The crane-flies (Tipulidae, Diptera). *Norsk Ent. Tidsskr.* 1: 296–7.

Kiefer, J. J. 1926. Chironomiden der 2. Fram-Expedition (1898–1902). *Norsk Ent. Tidsskr.* 2: 78–89.

Kirby, William, 1824. Land invertebrate animals (*In* Parry, Sir William Robert, Journal of a voyage for the discovery of a North-West Passage . . . with an appendix containing the scientific and other observations. London: 1821–24, 2 Vols.) Supplement to the appendix, pp. ccxiv-ccxix.

McLachlan, R. 1879. Report on the Insecta (including Arachnida) collected by Capt. Feilden and Mr. Hart between the parallels of 78° and 83° north latitude, during the recent arctic expedition. *J. Lin. Soc.* 14: 98–122.

Münster, T. G. 1924. Coleoptera, supplement. (*In* Alexander, Ch. P. Report of the second Norwegian expedition in the *Fram*, 1898–1902). *Norsk Ent. Tidsskr.* 1: 297.

Natvig, L. R. 1930. Culiciden der 2. Fram-Expedition (1898–1902). *Norsk Ent. Tidsskr.* 2: 358–9.

Strand, E. 1907–19. Coleoptera, Hymenoptera, Lepidoptera, and Araneae. (*In* Report of the second Norwegian Arctic Expedition in the *Fram*, 1898–1902, Vol. 1, No. 3).

Wahlgren, Einar. 1907–19. Collembola from the 2nd Fram Expedition, 1898–1902. (*In* Report of the second Norwegian Arctic Expedition in the *Fram*, 1898–1902, Vol. II, No. 10).

Distributional Problems in Alaska[1]

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ABSTRACT

The physiography and climate of Alaska are outlined. The fauna is divided into two main groups, a maritime coastal one and a continental interior one.

Three Merriam life zones are recognized: The Canadian along the southeast coast, main southern valleys and the low interior valleys; the Arctic in the Northern Coastal Plain, northern Seward Peninsula and thousands of high altitude areas; and the Hudsonian covering the rest of Alaska, and including large treeless areas especially near the Bering Sea. The relationship of the timberline to the Hudsonian or subarctic zone is discussed at length.

Distributional patterns of Alaskan insects are divided into two main groups, Beringian and Nearctic, depending on the evidence of a probable glacial refugium. Each group is further subdivided. Finally, a few of the major unsolved distributional problems are outlined.

PHYSIOGRAPHY

The physiography of Alaska is similar to that of western North America but rotated about ninety degrees counter-clockwise. From south to north there is a double coastal system of igneous mountains, an interior plateau mostly of ancient metamorphics, a sedimentary mountain system and sedimentary plateau and coastal plain.

The outer coastal mountains include some of the island ranges of south-eastern Alaska, the St. Elias, Chugach and Kenai ranges of the mainland, and the low ranges of Kodiak Island. The inner coastal mountains include the Coast range of the South East, the Alaska range and the Aleutian range. Between the inner and outer mountains lie a series of disconnected valleys of various widths. Many are submerged, but the most important ones are the valleys of the Copper, Gulkana, Matanuska and Susitna rivers and the lowlands around Cook Inlet. This system appears to be late Tertiary in age and has been heavily, and probably repeatedly, glaciated.

The interior plateau includes most of Alaska and the Yukon Territory. The plateau peneplain is of middle or late Tertiary age and lies at an elevation of about 6000 ft. in the east and lower in the west. Its dissection has proceeded to old age in the west, but in the east is young to mature. This area in Alaska has never been glaciated except for a few small local areas but only the westernmost part of the Yukon Territory escaped glaciation.

The northern mountain system, or Brooks Range, is a comparatively narrow strip which has undergone extensive glaciation.

The northern plateau and coastal plain is a low, fairly narrow strip of hilly to flat country which is unglaciated.

CLIMATE

The climate varies greatly. Summer average temperatures are 12°C. to 15°C. throughout most of the Territory, about 10°C in the Aleutians and Bering Sea coast and colder near the Arctic ocean. Winters are very severe with average temperatures below −15°C in all but south and southwest Alaska. Along the south coast and in the Aleutian region the winter temperatures average near 0°C, but become rapidly colder inland. Thus we find a highly continental climate in interior Alaska which grades into an oceanic one gradually in the flat Southwest but rapidly across the coastal mountains of the South and Southeast.

The chief moisture bearing winds are southwesterlies from the warm Pacific. These give heavy precipitation along the windward slopes of the coastal mountain systems. A small rain shadow is formed in the Copper valley and Cook Inlet regions and a much larger one over most of the Interior which, however, does receive some precipitation from the Bering Sea (Fig. 5).

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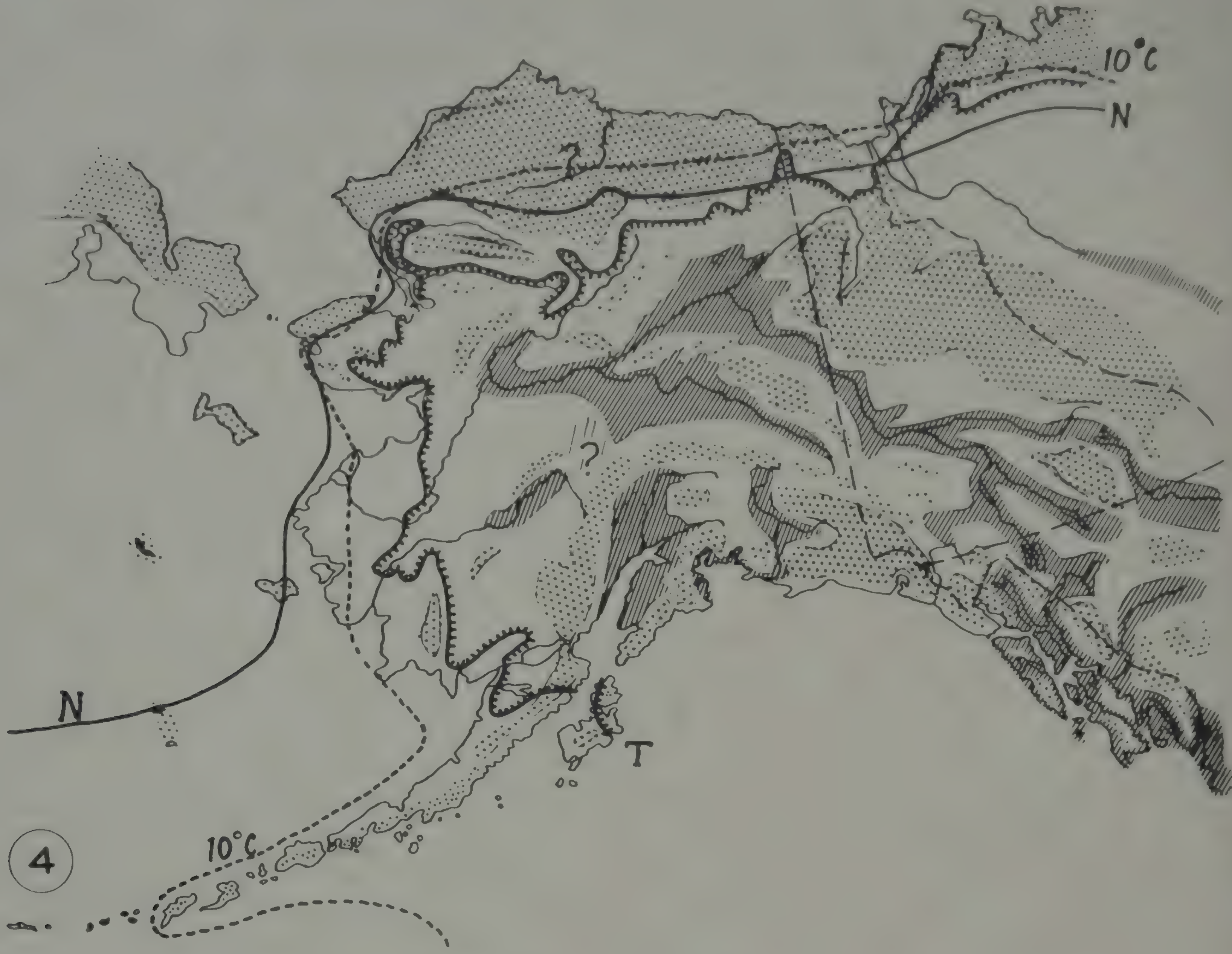

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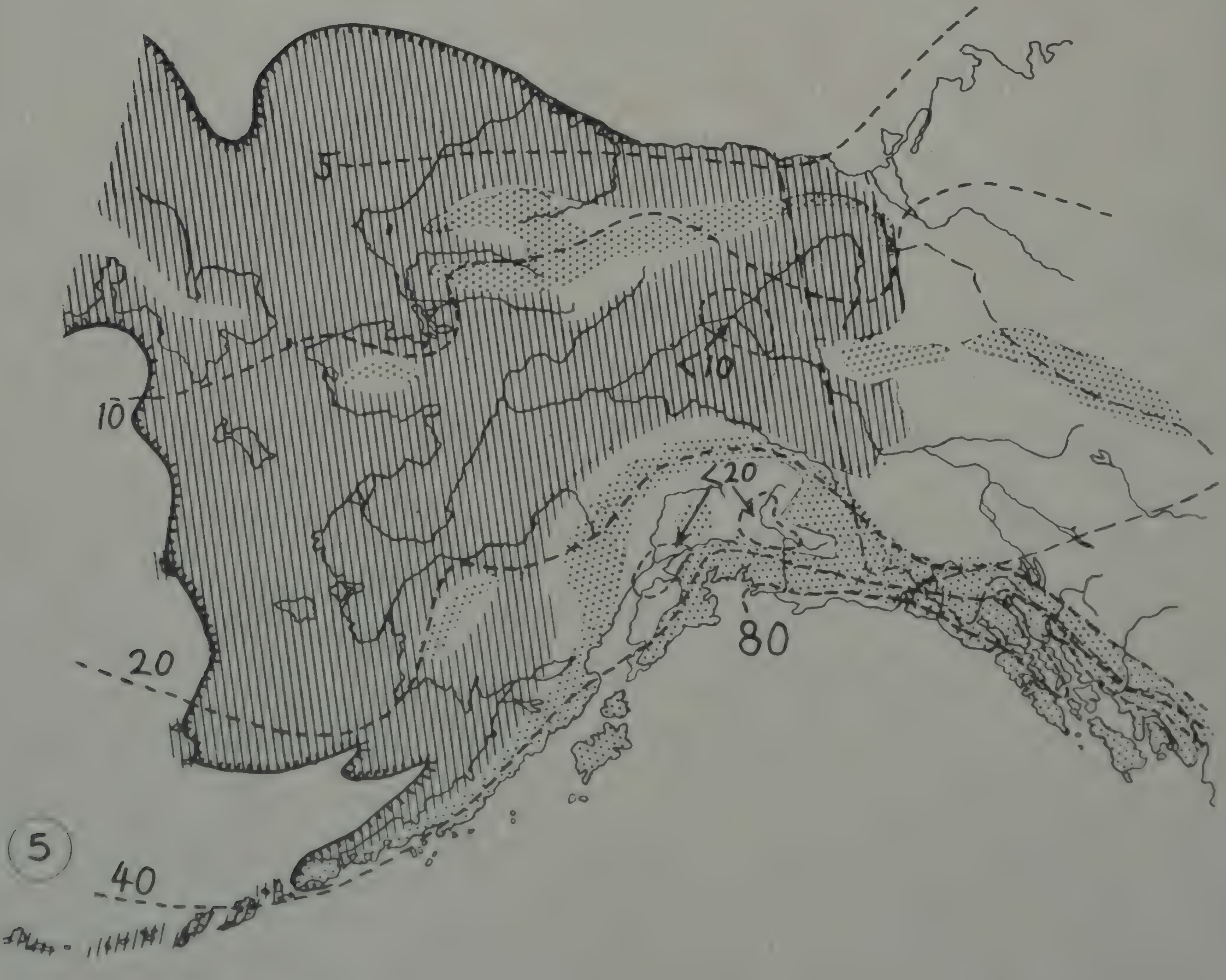
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The glaciated areas of Alaska are closely related to the areas of higher rainfall. The southern mountain system was heavily glaciated: the Interior escaped except for isolated ice masses in a few mountain ranges, most notably the Brooks Range (Fig. 5).

FAUNA

The fauna of Alaska may be divided into two main elements, a coastal one along the Pacific slope and an interior element occupying the rest of Alaska. The former is related to the coastal forest of western Canada and U.S.A. and the latter to the transcontinental boreal forest and tundra faunas. From the Kenai Peninsula eastward these two faunal elements are sharply separated by the great heights of the coastal mountain ranges, but near Cook Inlet and areas to the west they overlap, some coastal species extending northward along the Bering Sea Coast and Interior species extending out the Alaska Peninsula to the Aleutian Islands and some even reaching Kodiak Island.

LIFE ZONES

The Canadian, Hudsonian, and Arctic life Zones of Merriam are all represented in Alaska as shown in Fig. 4. The Canadian Zone fauna has two distinct elements: one the fauna of the heavy coastal forest (Western Hemlock-Sitka Spruce) in southeastern Alaska; the other the fauna of the richer parts of the interior forest (White Spruce-Aspen-Birch). An interesting association of the latter fauna is the grassland areas of the drier interior districts. These areas commonly occupy south-facing slopes and well-drained gravelly soils and resemble the aspen parklands of the Prairie Provinces.

The Hudsonian Zone occupies most of Alaska. It is characteristically an area of open dwarfed spruce forest with shrubby undergrowth rich in ericaceous or amentiferous shrubs and lichens. In the flora and fauna of this undergrowth lies the special character of the Hudsonian Zone. The so-called dominant forest trees usually cover only a small part of the ground and affect little the essentially open nature of the habitat. In contrast to this, the Canadian Zone is truly dominated by forest trees and the undergrowth is rich in mosses and herbaceous plants. It is essentially a closed forest, but open areas (except bogs) are usually covered in grasses and other herbs.

The upper limit of the Hudsonian or Subarctic Zone has been variously defined. The easiest and most commonly used criterion is timberline, in this region meaning the upper limit of coniferous trees growing upright to about the height of a man. This line (Fig. 4) excludes a broad territory along the Bering Sea, all but the extreme base of the Alaska Peninsula, and all the Aleutian Islands. In Northern Canada timberline is an extremely sharp biological barrier. The great bulk of the flora and fauna find their distributional limits within a few miles of timberline; only exceptional species occurring widely in both Arctic and Hudsonian Zones. Conditions in Alaska are profoundly different. Here, the great bulk of the flora and fauna of the wooded country continue beyond timberline for dozens or even hundreds of miles and continue above timberline in the mountains for many hundreds of feet. Most species whose northern limits are rather sharply defined by timberline in Eastern and Central Canada extend right to the Bering Sea coast and a very good proportion range into the Aleutian Islands. The limit of coniferous tree growth is quite clearly not a fundamental biological barrier in Alaska (Griggs 1936). It is of interest to note that deciduous trees (*Betula* and *Populus*) occur beyond coniferous timberline in Alaska. For instance, *Populus* trees grow north of the Brooks range and occur nearly 200 miles west of the limit of Spruce on the Alaska Peninsula (Knappen, 1929).

Another criterion is the July isotherm of 10°C. It may be seen (Fig. 4) that this line excludes most of the Bering Coast and the eastern Aleutians from the Arctic. A modifica-

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Fig. 4. Life zones (Merriam) of Alaska. Arctic zone, stippled: Hudsonian, blank: Canadian, diagonal lines. Nordenskiöld line, solid line marked "N": July isotherm of 10°C, dotted line: limit of coniferous trees, hachured line.

Fig. 5. The Beringian refugium in Wisconsin time, area with vertical lines; glaciated areas and oceans are not lined. Chief mountainous areas, stippled. Dashed lines, isohyets; annual precipitation in inches.

tion of this, the Nordenskiöld line[3] excludes the entire Aleutian region from the Arctic[4], but falls south of timberline in areas of strongly continental climate such as the Mackenzie Delta. The latter discrepancy has led Polunin (1951) to propose two modifications of the Nordenskiöld line: (1) at least fifty miles north of continuous forest (2) north of occasional trees reaching a height of 2 meters or more. This is the criterion here employed. It will be seen that large treeless areas (not counting arborescent deciduous species) are thus excluded from the Arctic Zone. It seems much more logical to regard these areas simply as "treeless Hudsonian Zone" on the basis of the very broad faunal and floral similarity rather than to place them in the Arctic with which they have little except a treeless (i.e. without conifers) condition in common.

The Arctic Zone, as above limited includes the Brooks Range and the area to the north, the northwestern slope of the Seward Peninsula, the Islands of the Bering Sea, and numerous high altitude areas throughout Alaska (Fig. 4). In central Alaska the timberline is about 3000 ft., but arctic conditions begin about 3500 to 4000 ft. Arctic conditions in Kodiak Island and the Alaska Peninsula begin about 1000 ft. The Islands in the Bering Sea have truly arctic temperatures, being colder than the Aleutians, both in winter and summer because the latter Islands benefit from the much warmer Pacific Ocean at their southern shores. The low sheltered valleys on the northern slopes of the Brooks Range pose a special problem. The fauna of these valleys appears to be an arctic one with strong boreal intrusions. For instance, half the breeding passerine birds are boreal forest species which do not occur near the coast. There are a large number of Palaearctic species in this area which occur nowhere else in North America. The barrier to their eastward dispersal is the low, forested Mackenzie Delta.

TIMBERLINE

The timberline in Alaska, as mentioned above, is very different from that of northern Canada (Fig. 1). In an excellent series of papers Griggs (1934, 1936, 1938, 1946) has compared timberline in southwest Alaska with that in the Rocky Mountains and New England. There seems little doubt that timberline in the Rocky Mountains has remained stationary for centuries, whereas that of most of western Alaska is rapidly advancing into treeless country (Figs. 2, 3). It seems logical to expect that the smaller plants of the Hudsonian Zone undergrowth, most of which attain reproductive age in one or a few seasons and many of which have light windborn seed, could advance into a favorable environment more rapidly than the slowly maturing, comparatively heavy-seeded conifers. The insects, of course, could mostly disperse at least as rapidly as the fastest moving plants. Thus it is not surprising, but rather to be expected, that the insect fauna of the subarctic forest will extend far beyond the trees in a region of moving timberline.

Timberline in northern Canada is a static or retreating one, having the usual stunted, crippled, and prostrate trees and also dead trees of about the same size and growth form (Clarke, 1940, Johansen, 1919). Under these conditions we find an abrupt change in fauna at the timberline.

The explanation for this anomalous condition so characteristic of southwestern Alaska does not lie in the oceanic climate nor in the heavy precipitation, for the phenomena

[3] A line expressed by the formula $V = 9 - 0.1k$ where V = average temperature (°C) of the warmest month and k = average temperature (°C) of the coldest month. This line falls to the north of the 10°C July isotherm in areas of maritime climate and is intended to allow for longer growing season in oceanic areas and also for the characteristic oceanic retardation of the summer maximum temperature until August (Fig. 5).

[4] It is interesting to note that the Nordenskiöld line passes north of the Pribilofs, which have a dominantly Arctic fauna. (Preble, 1923). This anomaly is probably easily explained by their post-glacial history. They must have received the bulk of their present arctic fauna in glacial times when they were part of the mainland, or at least much less isolated than now (Fig. 5). Their modern isolation makes introduction of subarctic elements obviously very difficult.

Figs. 1–3. Timber lines in northwest America. 1. Static timberline at 3000 ft. on the Franklin Mtns. near Norman Wells, N.W.T. (65°20′N, 126°30′W). Note crippled and prostrate living *Picea* and dead trunks of comparable development. Glacial erratics are visible in background.

2. Slowly advancing timberline near Eagle Summit (3500 ft.) on the Steese Highway, Alaska (65°30′N, 145°30′W). The hills and col on the horizon are arctic tundra (3700 to 4000 ft.). This is the unglaciated peneplain of the Yukon Plateau.

3. Rapidly advancing timberline at 3000 ft. near Paxson's Lodge, 50 miles north of Gulkana, Alaska. This is glaciated country typical of the southern slopes of the Alaska Range. Note that the trees are young and vigorous with no crippled or old dead trees visible.

occur also in dry, continental areas. It should be sought rather in the postglacial history of Alaska. Grigg's explanation that the forest trees have not yet had time enough to reinvade

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all suitable, but at present treeless, habitats seems quite tenable for the advancing coastal forest on Kodiak Island but fails to explain the same type of advance shown by the interior forest. The interior forest fauna and flora can have reached the glaciated Susitna and Gulkana valleys only by moving south through the passes in the Alaska range, yet it is in these very migration routes that the forest edge is now advancing most rapidly. One wonders, too, about a similar situation in unglaciated areas.

DISTRIBUTION PATTERNS

Distribution patterns of the Alaskan fauna fall into two major groups: the larger, those species which reinvaded Alaska from glacial refugia in North America; the smaller, those which survived glaciation in the Beringian refugium or Eastern Siberia. The two groups are clearly separable only in species with restricted ranges. The wide-ranging species may have found glacial refuge in central North America or Beringia and probably in many cases, in both areas. Some distributions of subspecies and species pairs give strong support to the likelihood of a dual refugium.

Nearctic Ranges

(1) A strictly coastal fauna, ranging from northern California to southeast Alaska and sometimes as far as Kodiak Island. This is a large group in the Coleoptera but is small in most other orders of Insects (Fig. 6).

(2) A large fauna which is coastal in Alaska but which occurs throughout southern British Columbia and extends through the mountains to Colorado and California. How far north the interior "leg" of this fauna extends is a mystery because central and northern British Columbia are almost completely unknown entomologically. Many species of this group extend as far inland as the Alaska Range and occur along the Bering Sea Coast to the Seward Peninsula (Fig. 7).

(3) A more widespread western fauna with typical cordilleran distribution outside Alaska and a general distribution in the warmer parts of Alaska. The more tolerant species typically extend to the Bering Sea Coast and Aleutian Islands. An interesting feature is the common occurrence of an eastern range extension in the Mackenzie Valley and northern parts of the Prairie Provinces (Fig. 8).

(4) The transcontinental boreal fauna, which covers most of northern Canada and the Rocky Mountains but usually avoids the wet coastal belt of British Columbia and southeastern Alaska. A peculiar but unexplained feature of this group is their frequent occurrence in the southwestern coastal parts of Alaska. The same phenomenon has been noted in plants (Raup, 1947). The paradoxical result is that southeastern Alaska has a fauna more "western" in affinities than southwestern Alaska. This transcontinental fauna may be divided into Canadian and Hudsonian Zone elements but such division in Alaska is weakly defined (Fig. 9).

(5) Widespread Arctic fauna, is mostly circumpolar and occurs at most localities of high enough altitude or latitude in Alaska and the glaciated sections of North America.

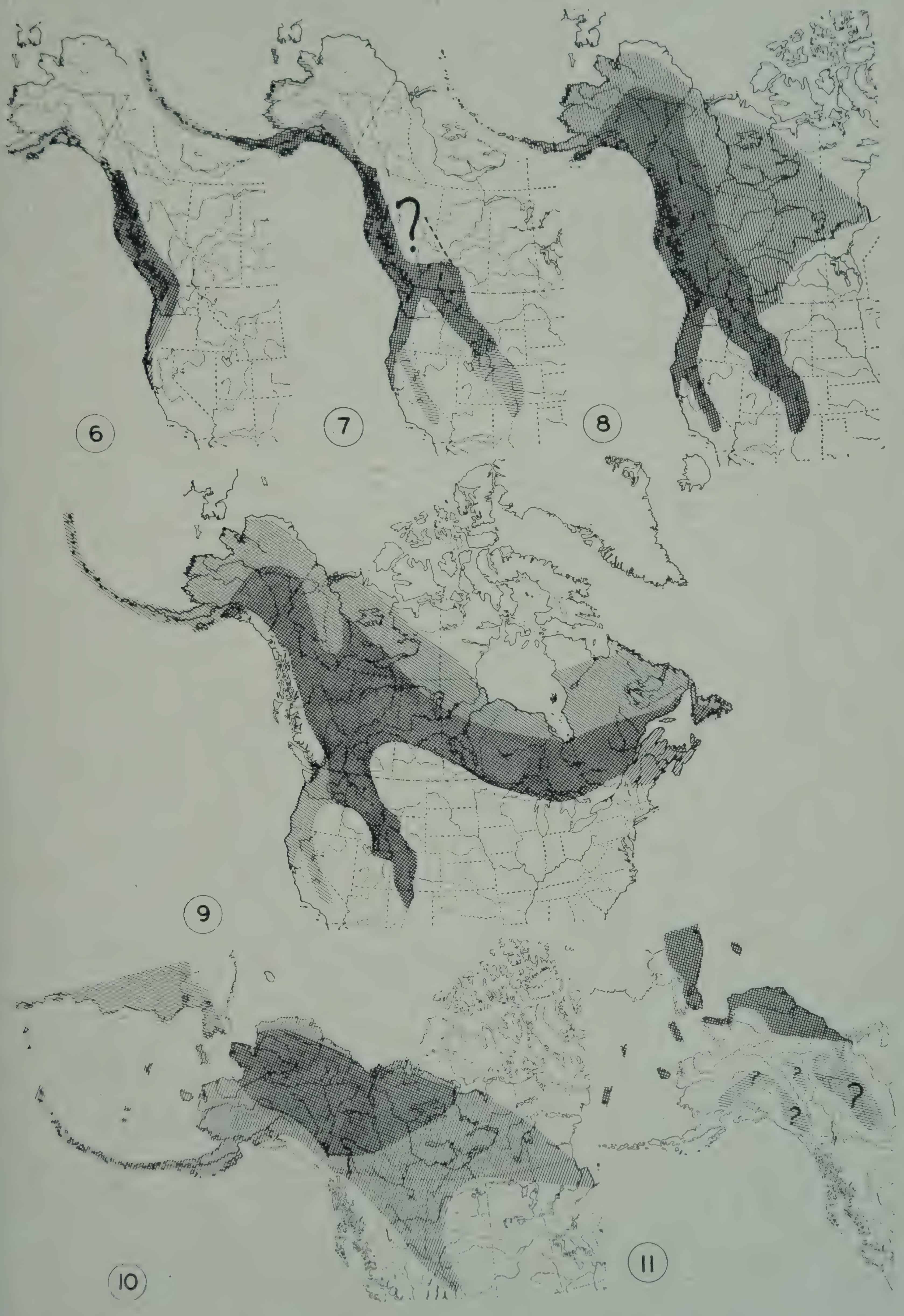
Beringian Ranges

There is little point in attempting to separate Beringian and Palaearctic groups here, since there was one enormous glacial refugium stretching from Alaska to France. There is at present (and probably was during glacial times) only a gradual replacement of some species and subspecies across the northern Palaearctic. The "Beringian or Amphiberingian" derivatives could more accurately be called eastern Palaearctic.

(1) The Aleutian fauna, centered on the Aleutian Islands and extending to Kamchatka and southern Alaska, is poorly developed in the insects but is an important one to the botanists (Hulten, 1937).

(2) The Interior Alaskan fauna is the best developed one in the insects. Concentric ranges based in the Yukon Valley extend eastward to the Mackenzie Valley and even to Hudson's Bay, southward down the Rocky Mountains to western Alberta, and westward into the Aleutians or across the Bering Sea to Siberia. This group merges into widespread Palaearctic ranges (Fig. 10).

(3) An Arctic Alaskan, or more properly, Old World Arctic fauna occurs in the northern slope of Alaska and Islands in the Bering Sea, and is probably of wide occurrence at high altitudes throughout much of Alaska. Its eastward dispersal is stopped by the



Figs. 6–11. Some important types of ranges of insects occurring in Alaska. 6, Pacific Coastal. 7. Coastal Alaskan—Rocky Mountain. 8. Boreal Cordilleran. 9. Transcontinental Boreal. 10. Beringian Interior. 11. Beringian Arctic.

subarctic Mackenzie Delta. Very little is known of its dispersal in the northern cordilleran region (Fig. 11).

CONCLUSION

The biogeography of Alaska is complex and much remains to be done before more than vague outlines become apparent. Very much more collecting is needed, and, equally important, the collections will have to be worked over. Stratigraphic work, especially pollen profile analyses and radio-active carbon dating, is needed from all parts of Alaska. A host of questions revolve around the puzzling relationship of the fauna to timberline. To state only a few: in what localities is timberline moving and how fast, and is the fauna also moving; has Alaska ever had a postglacial warm maximum, and if so, what is its bearing on present timberline-faunal relationships in areas such as the Alaska Peninsula and the inland parts of the Arctic slope? Some other unsolved distributional problems are: why so many interior species attain the Pacific coastal slope in southwestern Alaska, yet fail to occur elsewhere on the Pacific coast; why many species which are strictly coastal in Alaska become strongly continental further south and follow the Rocky Mountain chain, at what point the switch takes place and why at that place.

I hope I have given enough details to show that the zoogeography of Alaska is complex and unique. I hope also that my speculations have been sufficient to arouse your interest and to show how little we really know about the distributional problems of Alaska.

REFERENCES

Clarke, C. H. D. 1940. A biological investigation, the Thelon Game Sanctuary. *Nat. Mus. Canada Bul.* 96.

Griggs, R. F. 1934. The edge of the forest in Alaska. *Ecology* 15: 80–96.

Griggs, R. F. 1936. Vegetation of the Katmai district. *Ecology* 17: 380–417.

Griggs, R. F. 1938. Timberlines in the northern Rocky Mountains. *Ecology* 19: 548–564.

Griggs, R. F. 1946. The timberlines of North America and their interpretation. *Ecology* 27: 275–287.

Hulten, E. 1937. Outline of the history of Arctic and Boreal biota during the Quarternary period. Stockholm.

Johansen, Frits, 1919. The forest's losing fight in Arctic Canada. *Can. Forestry J.* 15: 303–305.

Knappen, R. S. 1929. Geology and mineral resources of the Aniakohak district. *U.S. Geol. Survey Bul.* 797.

Polunin, N. 1951. The real Arctic: suggestions for its delimitation, subdivision and characterization. *J. Ecol.* 39: 308–315.

Preble, E. A., *et al.* 1923. A biological survey of the Pribilof Islands, Alaska. *North Amer. Fauna* 46: 5–9.

Raup, H. M. 1947. Some natural floristic areas in Boreal America. *Ecol. Monographs* 17: 221–234.

DISCUSSION

C. H. LINDROTH. Highly desirable that terms of zones, e.g. in the Arctic be standardized in the Nearctic and Palaearctic. Is the "treeless Hudsonian Zone" of the speaker not the same as the low-arctic zone of Europe?

W. R. M. MASON. I agree it would be quite desirable but who will do it? I have used the nomenclature of Polunin whose term "low arctic" is about equal to the Scandinavian "regio arctica media". As you have said, much of the fauna of the "low-arctic" of Europeans occur also in wooded lower zones and I think it better to make the division further north.

R. I. SAILER. I agree with Dr. Lindroth in finding it hard to accept the treeless area along the Bering Sea as a part of the Hudsonian. If we accept this, might it not be better to abandon Merriam's life zone concept and adapt a scheme of biotic provinces based on those proposed by Dice for North America.

W. R. M. MASON. I think Dice's map should be modified by extending his Hudsonian province to the Bering Sea south of Cape Prince of Wales. But although Dice's provinces have much merit, I see no reason to abandon Merriam's life zones.

Southern Extensions of Arctic and Subarctic Insects in Bogs and Alpine Areas

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ABSTRACT

The long established concept of the isolated, southward existence of relict populations on high mountains is briefly summarized; and the truly arctic-alpine butterflies and some moths (chiefly of the Pyralid genus Crambus) *are listed. The arctic-alpine biota of the three chief North American mountain systems (Sierra Nevada, Rocky Mts., and Appalachian Mts.) are compared. Of these the Rocky Mts. have by far the richest biota, the Sierra Nevada the poorest. The less generally recognized concept of the very widespread existence southward of isolated relict islands of a subarctic (Hudsonian Zone) biota in acid bogs is given in some detail, illustrated by many records of Lepidoptera from the true, northern timberline zone, the timberline zone on mountains, and bogs at low altitudes as far southward as Colorado, North Carolina and Florida. The importance is emphasized of recognition of the acid bog as a distinctive type of habitat, and of not lumping it with such environments as marshes and swamps under an inclusive term such as "mire".*

The Original Faunal Connections Between Europe and North America

By C. H. LINDROTH
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ABSTRACT[1]

The number of animal species common to Europe and North America no doubt exceeds 5,000 and the insects are in the majority. Yet, almost half the species in common are due to human transport. Most of the species indigenous in both continents possess a more or less continuous circumpolar distribution. A special interest, however, is connected with the so-called Amphiatlantic (incl. "Westarctic") species which are lacking or have a broadly interrupted area on the Pacific side of the globe. They have often been used as arguments in favour of earlier Transatlantic land-connections. Attempts will be made to demonstrate that the cases of Amphiatlantic, and similar, distribution can be understood, partly by over-sea dispersal during present conditions, partly as remnants of a broken-up area of circumpolar type. The necessity, from a biogeographical point of view, for any kind of Transatlantic connection, joining Europe to North America, is thus denied. On the other hand, it seems inevitable to assume that part of the fauna of Greenland and Iceland immigrated across a Pleistocene land-bridge from the European mainland. An interesting point is that this invasion did not at all affect the fauna of Baffin Island which is completely devoid of a European element. Actually, the narrow strait between Greenland and Baffin Island is the most pronounced north-south limit within the arctic region of the Holarctic area.

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[1] Included in the book, "The faunal connections between Europe and North America", published by *John Wiley and Sons* in 1957.

On the Arctic and Subarctic Hemiptera of the Palearctic Region

By Håkan Lindberg
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My experience of the arctic and subarctic territories and their Hemiptera fauna is based only on field work in Fennoscandia. The information I can give regarding the conditions in the vast arctic and subarctic territories in north eastern Europe and in northern Siberia I take from older literature. It is also unknown to me whether the research of later decades has extended the knowledge of the Hemiptera fauna with regard to the abovementioned territories. From the limited literature of these last years no extra information of greater importance can be obtained. I have been informed that insect research in U.S.S.R. has attached less importance to the arctic and subarctic regions then to more southern regions.

In the work of Breddin "Die Hemipteren und Siphunculaten des arktischen Gebietes" of 1902 the arctic territory is restricted to the region beyond the timberline. In the palaearctic region lies an unconnected arctic tundra territory from the east of Fennoscandia, more definitely expressed on the little Peninsula Piscatorum and running along the north coast from the Cola Peninsula to the most eastern part of Siberia and some islands in the Bering Sea. Besides this, we naturalists working in Fennoscandia also refer to the arctic territory open woodless moorlands in northern areas which are disconnected from the continuous tundra belt. Thus there are, so to say, arctic islands along the whole Scandivanian mountain ridge. This opinion, which we hold in Fennoscandia, is based on the fact that these arctic territories are situated near to and form a continuation of the unbroken tundra territory. There is no sharp difference between this arctic or, so to say, arctic-alpine territory and the alpine zone further southward in Europe, as in the Alps.

The subarctic zone is situated between the woodless arctic zone and the northern evergreen forest, *regio silvatica*. The subarctic zone is above all characterized by the more or less bushy field birchtree, a kind of *Betula pubescens*.

In the subarctic bushy forest the vegetation, in many cases is rich, and consists of herbs and shrubs. The evergreen forest boundary, that is the northern boundary for *regio silvatica* in Fennoscandia, is made of *Pinus silvestris*, further eastwards of *Picea excelsa*. The arctic islands along the scandinavian mountain ridge are mainly surrounded by the continuous subarctic zone.

Now that I have explained our opinion of the zones in question, I will make a short summary of the Hemiptera, which are to be found in those zones.

According to Breddin there are no arctic Hemiptera species, but he regarded only the continuous tundra as the arctic zone. He found that the species of the tundra territories also exist outside the tundra—southwards. These species could not, therefore, be called arctic. Referring to the opinion that the woodless fjeld-moorlands in northern Scandinavia can be assigned to the arctic region, I wish to point out that, in my opinion, at least two species of Hemiptera, the saldids *Chiloxanthus borealis* Stål and *Calacanthia trybomi* J. Sahlb. can be regarded as arctic. Besides in arctic Siberia these species occur rarely on the barren fjelds in most northern Fennoscandia. *Chiloxanthus arcticus* J. Sahlb. can be placed in the same group, but its systematic position is up to now somewhat unclear. It is an important fact that these arctic Hemiptera species belong to the family Saldidae; also in high mountain territories, e.g. in the Alps, and in mountains of Central Asia, the Saldids seem to live at the upper boundary of insect life.

In the arctic zone one finds some other Hemiptera which, however, can also be found and presumably exist mainly in the subarctic or evergreen zone. I have found *Salda opacula*, *Gerris asper*, *Sigara carinata*, *Callicorixa producta*, *Psammotettix frigidus* and *Calligypona alpina* in this zone. Sahlberg mentions from the arctic zone in Siberia the Saldids *Teloleuca bifasciata* and *pellucens*, among Mirids the peculiar *Platypsallus acanthioides*, *Orthotylus discolor* and *artemisiae*, *Chlamydatus wilkinsoni* etc.

The sparsely occurring Hemiptera species belonging to more southern parts of the arctic zone, made Breddin conclude, that the arctic zone is only an annex of the subarctic and evergreen zones, in which the fauna has been impoverished. I, however, wish to say that also the occurrence of the Hemiptera supports the presumption that *regio arctica* forms its own zoogeographical zone. I here refer to the above mentioned Saldids. Furthermore, with the inhabitants of this zone could be included the earlier mentioned Mirid *Platypsallus acanthioides*. Besides, in arctic Siberia these species are found by Ponoj on Cola Peninsula, which apparently lies in the arctic zone.

If insect-species regarded as subarctic have to be found only in the subarctic zone, in accordance to the definition given, it should be hard to find a good example of a subarctic insect, at least among the Hemiptera.

I have, however, found in the north Fennoscandian fjelds and on the boundary of the tundra on Peninsula piscatorum, that many Hemiptera species in maximal abundance occur right in the fjeld birch tree forest and on corresponding levels. Even if they can be found in adjacent parts of the arctic zone and in the evergreen forest, I am inclined to consider them as subarctic. I would like to extend this conception and also refer to this group of insects such species, as live mainly in the northern parts of the evergreen territory on the boundary of the subarctic zone. Thus, if we consider this subarctic concept more broadly we can refer quite a few species to this group of subarctic Hemiptera. I can mention the following: (To this group should not be referred species which belong completely to the northern part of the evergreen zone, we call them high boreal.)

Nysius groenlandicus
Teratocoris viridis
Chlamydatus wilkinsoni
Teloleuca bifasciata
T. pellucens
Saldula scotica
Sigara carinata
Callicorixa producta
Diplocolenus limbatellus
Thamnotettix confinis stupidula
Calligypona alpina
Psylla betulae-nanae
P. palmeni
Orthezia cataphracta

The so called subarctic species are consequently spread in a belt which extends as a comparatively narrow zone between the arctic fjelds or tundra territories and the continuous evergreen forest zone. Among the material from such a transition territory in Fannoscandia at the Arctic Ocean which consist of 81 Hemiptera species I found 14 subarctic species, 15 which I marked as boreal, and 52 species with a vast spread southwards. In territories which I signify as the arctic zone I did not find any arctic species, whereas in the same zone some boreal species and species with a wide distribution could be found. In the evergreen zone I discovered 8 of the 14 subarctic species.

It is mostly among the subarctic Hemiptera one finds so called boreoalpine species. I have already mentioned the 3 most typical examples of such among the Hemiptera. I would like to mention them once more, especially as not enough attention is paid to them: *Saldula scotica*, *Sigara carinata*, *Callicorixa producta*. These boreoalpine species occur in the subarctic zone (in a wider sense) in Fennoscandia and eastwards, because as far as I know, they can be found over the whole of Eurasia. Furthermore, at least a part of them occur in Scotland and in the Alps. Whether they can be found in corresponding Asian highland territories I do not know. I can mention some more territories of the spread of the species in question, namely the cliffs facing the open sea along the east shore of North Sea, in the middle part of the Baltic Sea and the big Lake Ladoga. (During a journey in Canada I had the pleasure of seeing from the train the rocky north shore of Lake Superior with cliff islands. Both the edaphic and climatic factors make it possible that subarctic Hemiptera species with a distribution corresponding to that of the European boreoalpine species may be found along the shore.)

Knowledge of the arctic and subarctic insect fauna of North America has increased very much lately. Unfortunately, I have not had the opportunity of studying more closely the literature regarding this. In any case publications on the Hemiptera fauna of the arctic and subarctic zones in North America are very scarce. A comparison between the Hemiptera fauna of the northern zones of the old and new worlds is very much wanted: they certainly have species in common. The until now known cases of a holarctic spread, however, concerns species with a somewhat more southern occurrence, mostly species belonging to the evergreen zone. In the material of Heteroptera collected by Scandinavian entomologists in Newfoundland which I have received for examination, there are many species with a holarctic distribution, but only one of them I should quite definitely signify as belonging to the group of arctic or subarctic species, namely *Teloleuca pellucens*. In the material furthermore there is *Saldula opacula*, which also has a northern distribution, but should be regarded as boreal, hardly as high boreal. Please notice that the last mentioned species belong to the family Saldidae which has been mentioned in this lecture many times. Besides, the material from Newfoundland includes many other Saldids, but these are nearctic.

The Hemiptera fauna in the arctic and subarctic zones is poor, but comprises special species. In the greater part of these zones the Hemiptera fauna is very little known and one has a more detailed knowledge only of the arctic and subarctic zones of Fennoscandia. A summary of the Hemiptera fauna in question should be made, but before that research into this fauna should, if possible, be made in territories partly or wholly unexplored.

Origin and History of the Insect Fauna of the Northern Palaearctic

By Georg Warnecke
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ABSTRACT

These conclusions are based on the following suppositions: (1) Monotypic origin of species; (2) Ecological vigour is almost the same, at least in recent periods; (3) The limits of distribution are essentially settled.

The origin of the present fauna and flora of the Holarctic Region is the Angara Continent, the old land mass in Eastern Siberia and China. From here it expanded to North America, Asia and Europe. At first, there was a maximum conformity but during the glacial periods this was strongly disturbed, the different degrees of impoverishment being mainly due to the directions of the high mountain chains. In North America the animals and plants could give way toward the south; in Europe, they were pressed toward the unsurmountable barrier of the Pyrenees, Alps, etc., producing an extreme decimation of the fauna and flora. The resettlement in North America was made by the former stock; in Europe from the remainder of the later pleistocene fauna and from new immigrants out of western Asia and Siberia. The north-south extension of the mountains in North America seems to have made only comparatively slight variations between the East and West. In Europe, however, the separated southern situation of the high mountain chains has produced a peculiar type of distribution, that of the boreo-alpine species. There are about 200 species of animals that are found in northern Europe and in the high altitudes of the southern mountain chains but are missing in intermediate places. These species lived during the pleistocene in the tundra zone between the Northern ice and the glaciers of the southern mountains. With the final retreat of the ice one part of the species followed the withdrawing ice towards north Europe while the other part of the same species retreated into the high mountains. This cannot be said of Asia and North America. In North America there are minor analogies in the relict fauna of the White Mountains of New Hampshire, etc.

The summary of these statements is thus: In comparison with North America it is not the simple "staying behind" of northern species far in the south that is characteristic for Europe, but the exchange of cold-adapted species between the north and the south, thus the shifting of arctic species to the southern high mountains and shifting of southern alpine species to the high arctic and in this way producing the great mixture of different fauna elements in Europe.

I have to make some statements in advance: For a long time zoo-geographical research suffered through want of unobjectionable evidence, and, moreover, it led to wrong conclusions for want of solid determinations. Inaccurate and systematically false taxonomic, faunistic, and ecologic statements have been the cause of confusion, and, hence, zoo-geographic research is often met with distrust, especially historical zoo-geography. These investigations are not free from speculations. But one cannot try to explain the distribution of animals simply from their range in our days. Certainly, the limits of the range of a species as well as the manner of its distribution within the area of extension are determined by ecologic factors in their widest sense, and likewise so by morphologic (also psychic?) qualities of the species. As to the totality of the range, however, this can only be understood and explained as something historically grown (Reinig, 1937; Rensch, 1952). For, indeed, the present state is but a transitory one, and as such it is present and future in one, thus representing only the bridge between a fixed, though mostly buried passing of the past and of a future which is totally in the dark. This past which, indeed, makes the present fully comprehensible, can be elucidated.

There is no reason for mistrusting historical zoo-geography. As to the importance of ecologic zoo-geography, I may add the following. What exactly is the extent of knowledge of the ecologic and physical factors relating to correlations of an animal to its surroundings in any individual case? And even if, by most careful studying, most of the individual factors were ascertained, what is the extent of knowledge concerning their mutual influence and their entire effect? There is no doubt, ecologic zoo-geography—in earlier times—took things easy by restricting itself to one major factor alone, e.g. heat or humidity. Such a simplification may be possible in very few instances such, as oceanic animals which are stenothermic at least in some stages of their development. As to the thermal factor, I may as well point out that in this case work is being done with the standardised figures of the meteorological institutes. The values thus gained provide at best an average climate, but, unfortunately, most of the plants and animals don't live in it. Hence the numerous experiments made for comparing area limits with the progress of certain climatic lines, isotherms mostly, and so constructing an inner connection by means of some essential conformity, are as a rule open to criticism. For fauna and flora it is not the average temperature which is of importance, but the extreme values. I am aware that the "life zones" which figure so prominently in North American literature, are mostly based on the average temperatures of the different areas and the "rainfall-zones". But do they take the animals in consideration too? Should there not be more frequently than so far it seems to have happened, be made complete by consideration of the temperature extremes and the complexity of the surrounding conditions? Also must one not forget that widespread species, by forming eco-types, may live within vast climatic regions which in themselves may vary most strongly.

The most important presuppositions of historical zoo-geography ought to be briefly mentioned:

(1) No polytopic origin of species and of superior units, although local types may develop polytopically.

(2) The constancy of ecologic valency of the species, i.e. the adaptability to a sphere of existence. It has to be accepted as probable that those species which, at present are characteristic for certain regions of the world, must also be regarded as characteristic for corresponding regions in prehistoric times. This must certainly be valid for the last earth periods, and not only for the obvious morphologic adaptability to one certain life-zone (e.g. saltatory rodents in the steppes), but also for an adaptability which cannot be established either physiologically or morphologically. Here, in order to avoid any doubt, I will point out an example of an animal securing extension by a change of biotopes. The Geometride *Larentia didymata* L. in central Europe inhabits shady deciduous woods, but in the Faeroers, the woodless islands between Scotland and Iceland, it flies about on meadows in the open country. It would be rash to conclude that such a case represents a change of ecologic valency. One might explain this incidence by saying that an adherence to certain conditions of light might be the decisive factor, and *Larentia didymata* finds these conditions under the cloudy sky of the Faeroers even without the protection of trees. Lindroth (1931) pointed out the same appearances under seemingly new conditions and in quite different localities. Maybe one doesn't call it "ecologic adaptation" in these cases, but rather an invasion of substitutional biotopes which still conform to ecologic valency, and it must be left to the investigation of individual cases whether there has really occurred a fundamental change of this valency.

(3) The range of most animals is a confirmed fact, and there is but an insignificant fluctuation at the boundaries. This comprises also all highly vagile species, especially those of strong flying capacities, a fact often overlooked in former times. Nearly all animals are connected with certain "life-zones" by an enormous number of ecologic demands. They are tied to them exactly as the plant is connected by its roots to the soil in which it grows. Even mobile species are not too inclined for long distance travelling, as is sometimes supposed. One ought to take into consideration the behaviour of the animals, which so far has been studied only negligently, e.g. the birds' adherence to their home, which may be of a psychical nature.

Otherwise, those biotopes attainable by the normal possibilities of extension of the different species, and congenial to them, would long since have been colonised.

And now to the subject of my lecture:—

The origin of to-day's fauna of the Palaearctic and the Nearctic—I can only refer to the prevailing opinion—is in the Angara Continent, by which we understand that very ancient region of eastern Siberia and China that has not been covered by sea since the early palaeozoic period. From this centre a fauna still recognizable as uniform has spread to the west as far as Europe, and to the east as far as North America. It may here be mentioned that, according to the theory of Wegener which is nowadays acknowledged in its essential features, in the northern hemisphere the continents were connected till into the early tertiary. Thus a general extension across the areas of the northern part of the globe was possible. By migrations from one centre over then still connected regions we may, therefore, come to explain without difficulty the uncontestable and very far-reaching homogeneity within the northern part of both the old and the new world as to their fauna and flora, and, hence, we may neglect the supposition of polytopic development or either of landbridges.

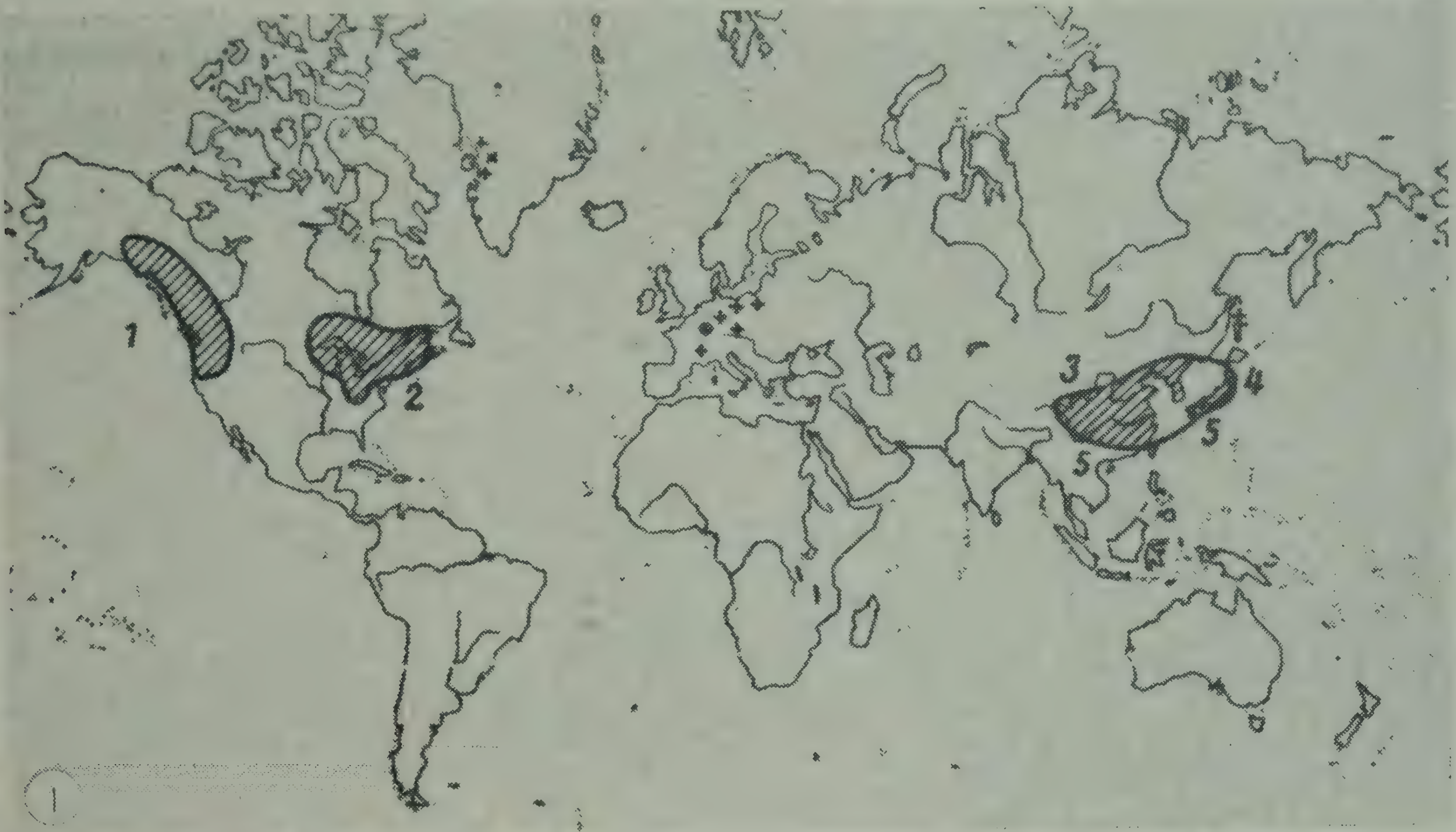


Fig. 1. Distribution of the genus *Thuja* (5 species). Hatched: Present distribution. Cross: Tertiary evidences. Cross with circle: Interglacial evidence. (Walter).

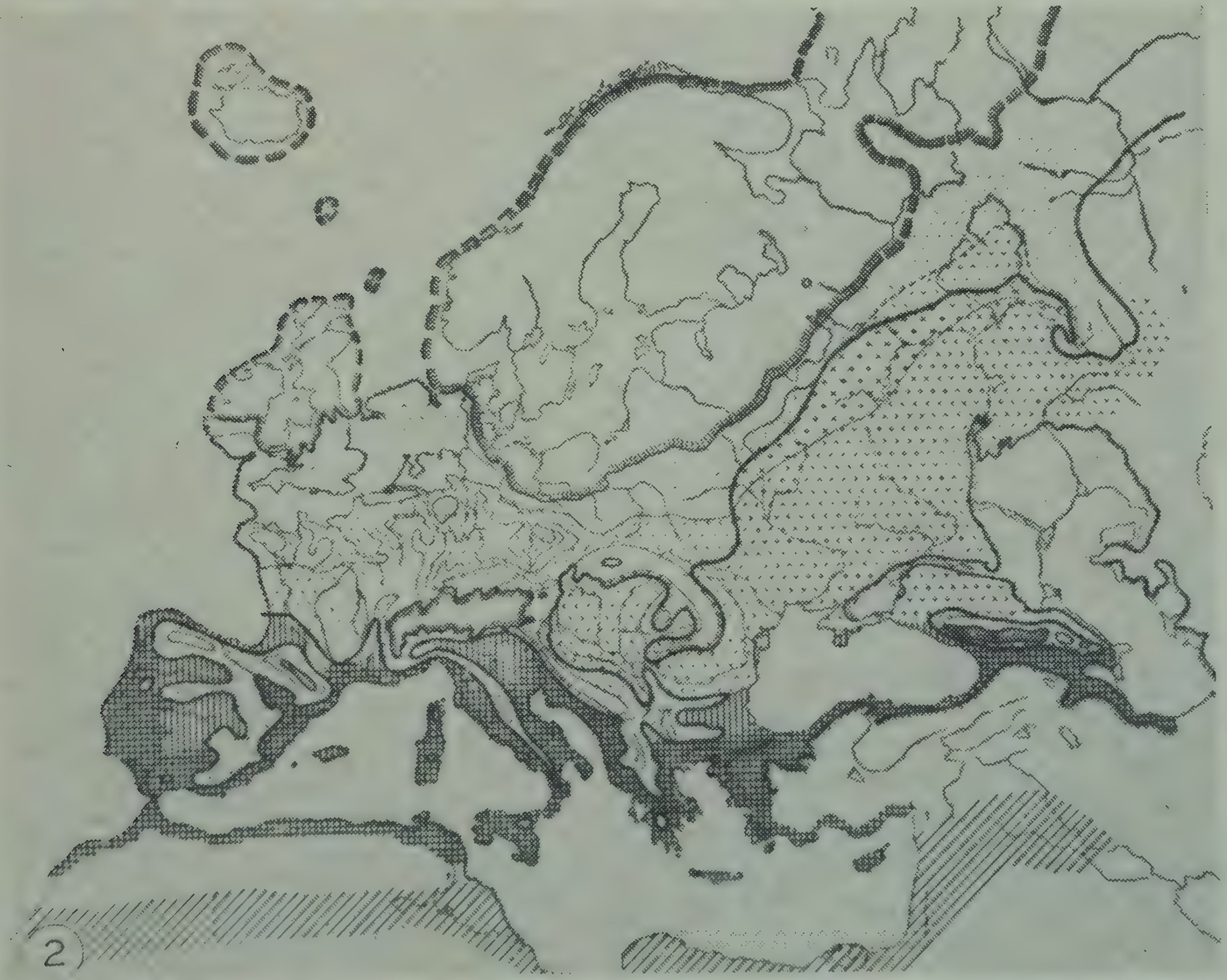


Fig. 2. Hypothetical life zones of the latest ice age (Würm) in Europe. Hachured outline: Würm glaciation. Lines with dots: Coasts during the ice age. Lightly and heavely stippled areas: Tundra and steppe. Perpendicular lines: Forests without warm-adapted vegetation. Crosshatching: Forests with warm-adapted vegetation. Oblique lines: Mediterranean vegetation. (Walter).

From the far-reaching conformity of both the fauna and flora of northern Asia, Europe, and North America, it may be well explained, why a vast number of families and orders of plants and animals are characteristic for these regions round the north-pole, while they are absent from the remaining parts of the globe. We have sufficient reason, therefore, to collect the whole region of both the palaearctic and the nearctic as a holarctic one.

The faunistic conformity of this holarctic region has been securely established by the fact that all over its entire space it embraces three climatic regions, each of which contains three equal districts of fauna and flora.

(1) North of the timberline arctic tundras (arctic region, tundral). There is reason to assume that the tundral fauna formed its present shapes during the glacial periods. Many orders and species have a circumpolar range.

(2) A forest region (arboreal), most noticeable in Siberia and in Canada, namely in the northern parts of both hemispheres as a belt of coniferae, known in Siberia as the taiga, and more to the south a summer-green region of deciduous woods. This latter holarctic zone does not circle the globe like the tundra and the pine-belt-zone, but is only found in eastern Asia, in central Europe and in the eastern states of the U.S.A.

(3) Regions of steppe and wastes (eremial) in central Asia, in northern Africa, and in middle North America.

Botanists are fortunate in that they are able to prove the extensive floristic conformity of the entire holarctic by fossil species dating from earlier earth-periods. Palaeontological investigation in Europe and North America has already largely shown that many orders of plants were formerly common all over the holarctic, and especially that they were indigenous in Europe as well. For example the following genera may be mentioned: *Thuja* (Fig. 1), *Juglans*, *Liriodendron*, *Liquidambar*, *Hamamelis*. The number of plants and their orders which at present are missing in the European-Asiatic region may be more than a hundred (Walter, 1954). It may be left open to ask whether they are the same species which once covered the circumpolar region.

We have no reason to suppose that the distribution of the fauna in the holarctic should not also have been circumpolar as regards most of its orders and species. All over the northern globe there have existed, and, indeed, far back as the pleistocene, even arctic species, like the musk-deer.

This uniformity of the holarctic fauna has now been most strongly disturbed and changed through the glacial periods of the pleistocene. Even if, on the whole, the faunistic character of the holarctic has been preserved, yet there has been a different course of development in the palaearctic and in the nearctic owing to the influence of glaciation, and so Europe's fauna came to have its own history. In this connection the glacial periods of the pleistocene may be looked at as a uniform procedure.

This phenomenon has had its strongest effect in North America and Europe, but was less in northern Asia. North America as well as Northern and central Europe were covered far to the south by an ice cap and the alpine mountains were glaciated. For Europe I give the picture of the largest extension of glaciation; it is the time of the last ice-period, Riss glaciation (Fig. 2). And as to North America I show a picture of the Wisconsin ice-period (Fig. 3, Dillon 1956).

The consequences of these glaciations are well-known: they lead to the displacing of fauna and flora to the south, to the complete desolation of the vast ice covered regions, and to the extension of the tundras down to the fiftieth degree of latitude north (in North America even further), and to the widening of the Eremial. The deciduous woods receded far back into refugial regions. The largest of these arboreal refuge regions were in eastern Asia, in Europe in the Mediterranean zone, and in North America in the south-eastern Atlantic States, the north-western Pacific States, and in the highlands of Mexico.

Now what sort of fauna was it that was afflicted by these effects of the pleistocene? It was the ancient arcto-tertial fauna, which, however, to be sure was no longer a uniform one. On the one hand it must already have contained arctic, that is extreme northern elements, on the other also alpine species, which means species of the high mountains. Generally it is supposed (especially as regards the flora) that these two elements have de-

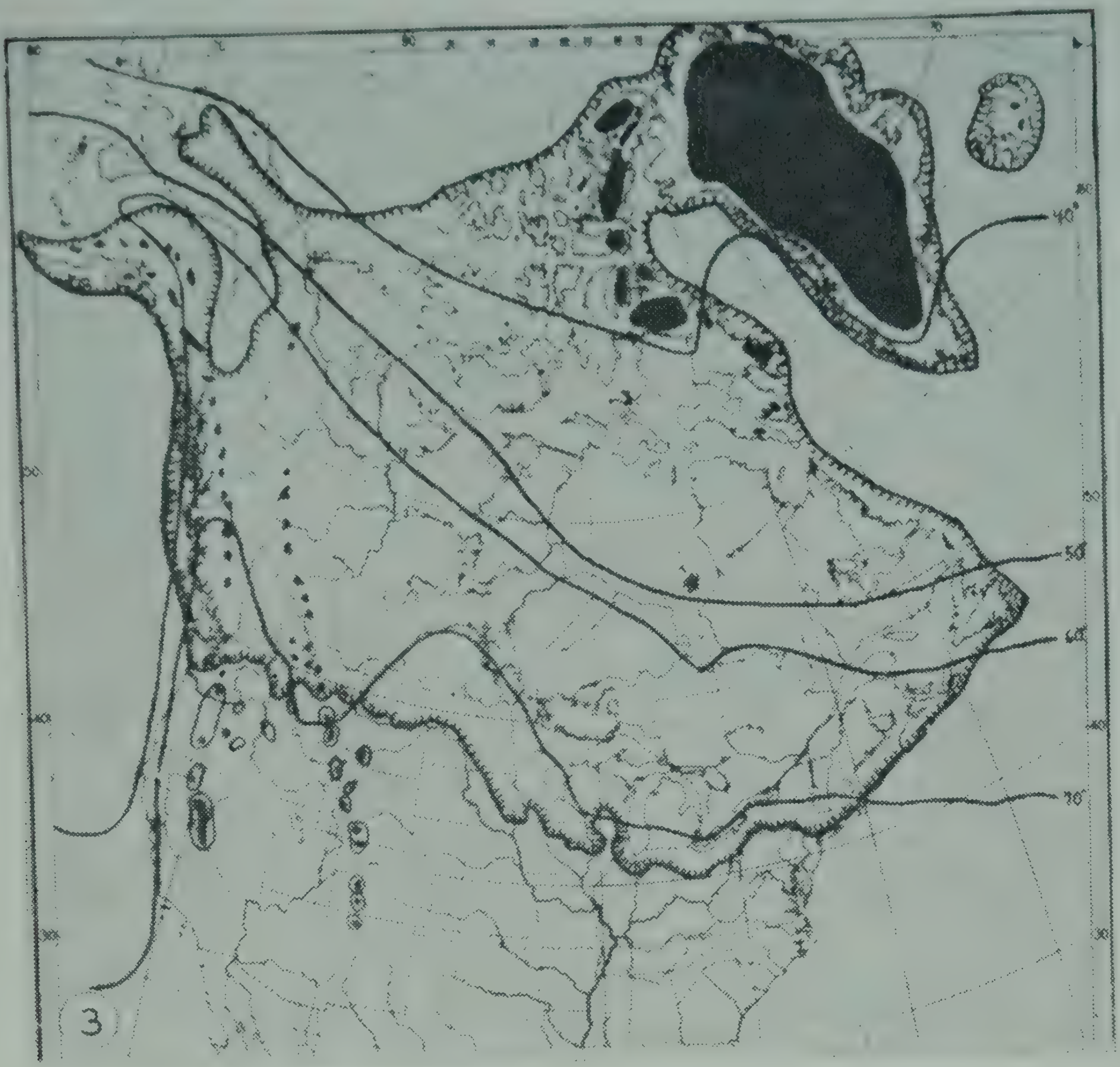


Fig. 3. Glaciation of the Wisconsin ice age. Black areas: Existing glaciation. Hachured outline: Wisconsin glaciation (Dillon).

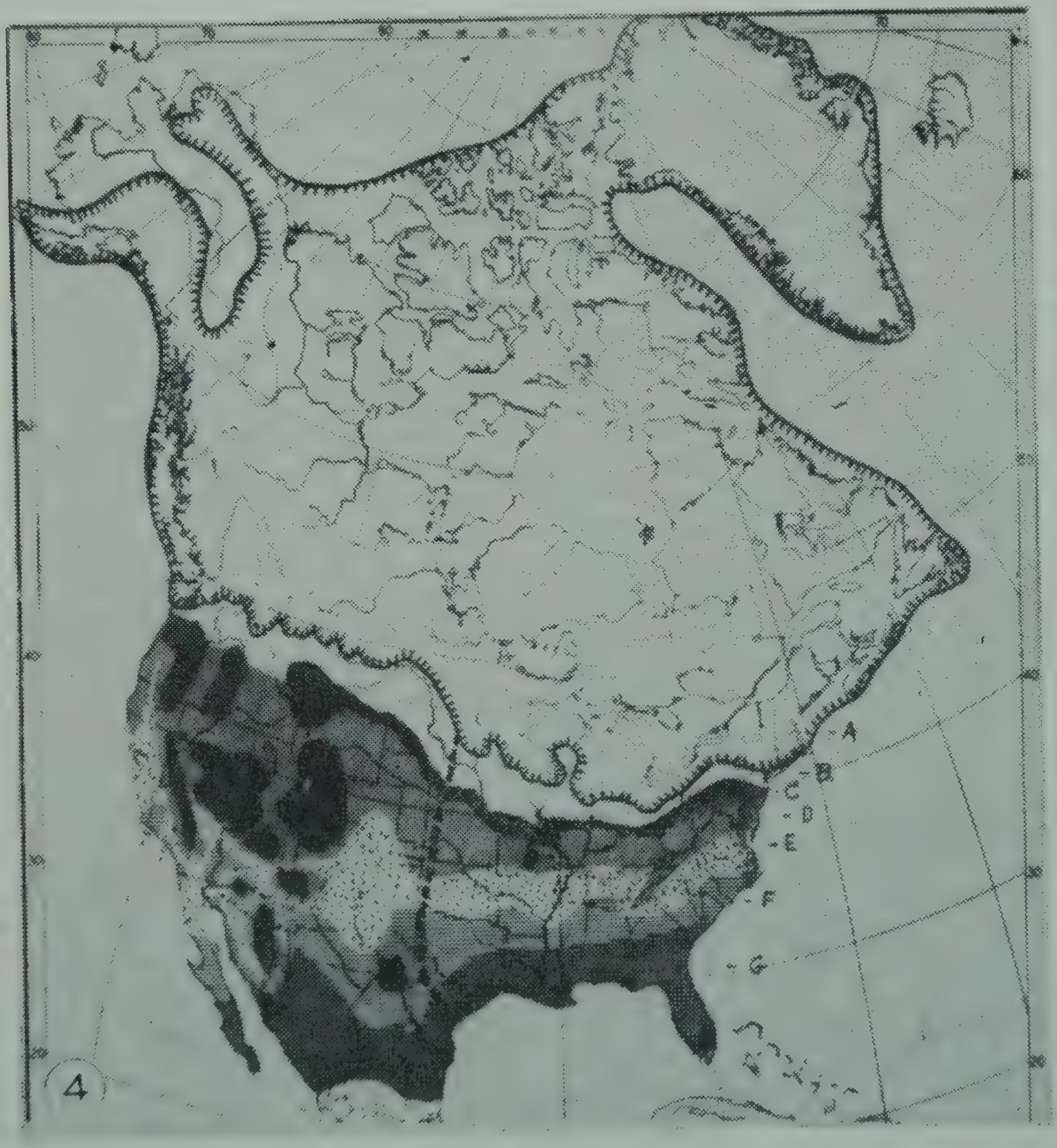


Fig. 4. Hypothetical life zones of the Wisconsin ice age. A: Arctic glaciation. B: Tundra. C: Hudsonian. D: Canadian. E: Transitional. F: Upper Austral. G: Lower Austral. H: Tropical. (Dillon).

veloped independent of each other. I am not convinced that this is the case with the fauna. There are no individual arctic orders, decidedly not among Lepidoptera. And even those butterflies characteristic for the arctic, have their nearest relations among palaearctic alpine species. I may mention the *Oeneis*-species. Alternatively they belong to orders with exceedingly different valency (Colias). Thus the arctic species are likely to be of alpine descent originally; and seem to have been formed as alpine species in the high mountains of the northern half of Central Asia (from Thien-Shan to the mountains on the lake Baikal). Later they became distributed holarctically and have developed different species in the arctic. However, this differentiation is certainly very old, so that both elements may be distinguished from each other, not by their descent, but their actual range. During the eocene, with the formation of the last high mountains (especially those of the Alps in Europe), there has obviously been another transformation and evolution of alpine species, for instance those of *Erebia*. There has obviously been no similar process in the arctic. Hence it would be better to call those species living in the arctic and its surroundings, but missing in the southern high mountains, *only* arctic species and *not* arctic-alpine species. And it would be better to call the species of the high mountains alpine species. But, of course, there are species which can be called according to their distribution arctic ones *and* alpine ones.

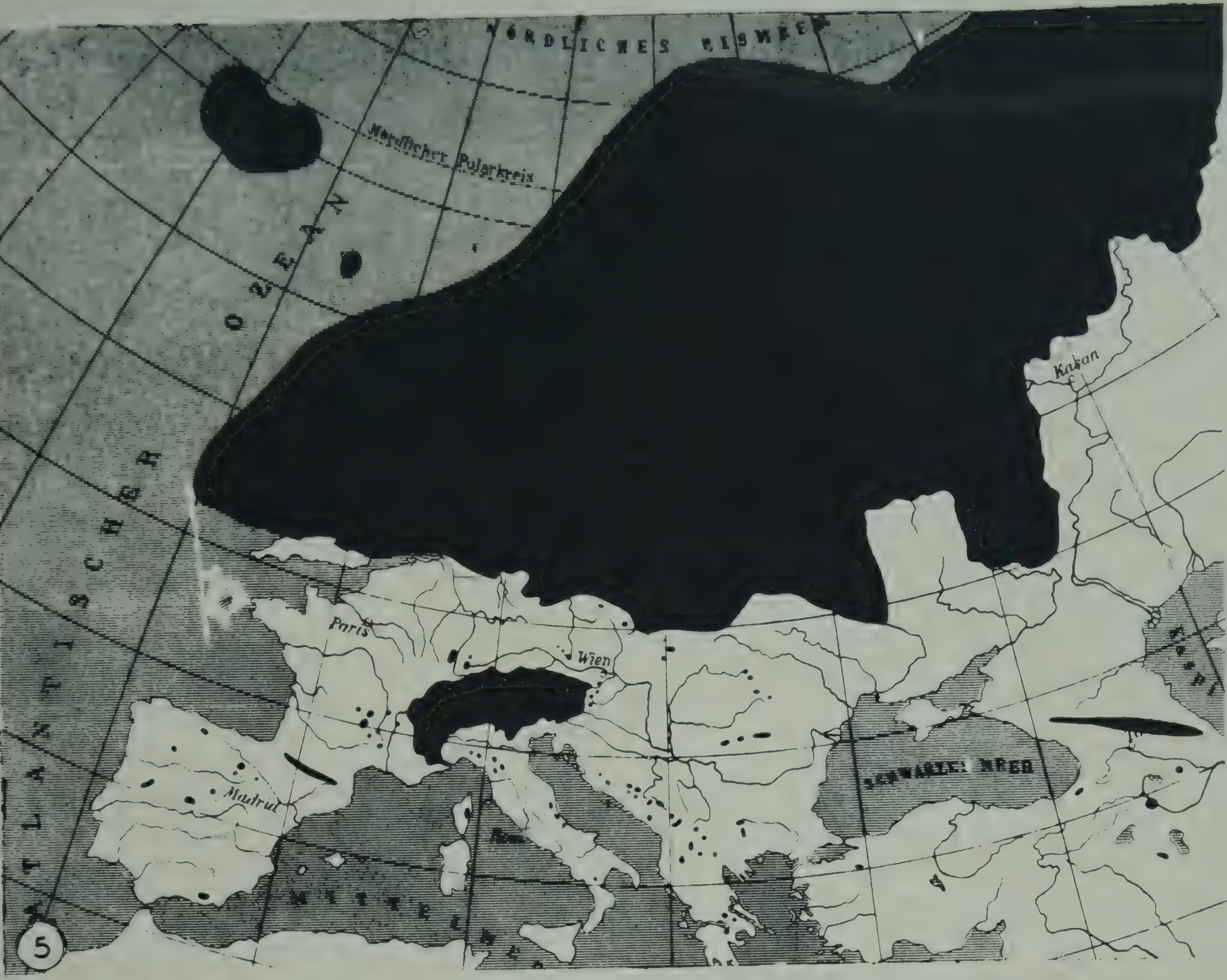
The glaciations of the glacial periods have now led to contrasting effects in Europe as against North America. They are the natural consequence of the different trend of direction of the high mountains of these two regions.

In North America the course of the mountains goes north-south, whereas in Europe the course of the southern mountain ranges is west-east, as for instance with the Pyrenees and the Alps. That means in North America the fauna and flora pushed on by the advancing ice could retreat unhindered over vast regions towards the south (Fig. 4). In Europe, however, plants and animals were pressed against those high mountains transversing their avenues of retreat (Fig. 5). Being heavily glaciated right into their forelands, they proved unsurmountable barriers for a vast number of plants and animals. For that reason, in North America the several fluctuations produced by the separate glacial and warm periods have not really played an essential part in the retreat and the re-immigration of the *stock* of the fauna itself. The question, as to how far the *distribution* of the separate species has been influenced by it, may here be left aside. In Europe, though, these repeated pressures against the high mountains have caused an extraordinarily strong decimation of fauna and flora. Those animals and plants which were unable to overcome these barriers, became extinct. This decimation of the flora which intensified increasingly till the end of the pleistocene, can be demonstrated especially by pollenar-analytic investigations. But deposits of the pleistocene and the late pleistocene period have also proved the same for the fauna.

Regarding the fauna I should have liked to give you the number of species in Europe and that in North America for certain genera of butterflies as *Oeneis*, *Lycaena*, *Plebeius*, etc. but as long as the views of the "splitter" and the "lumper" are so different such comparisons are of little value. I can only say that in Europe there are perhaps 340 species of butterflies while Klots (1951) mentions 442 species alone for eastern North America.

I consider it important to analyse more thoroughly the nearctic and palaearctic species in regard to their specific relationship to be able finally to establish a comprehensive taxonomy. This has not been accomplished in many cases due to the lack of material for such a study. I am referring this for instance to the Siberian and American species of the genus *Oeneis*, and furthermore to some of the *Erebia*. The *Boloria pales* group (there are four distinct species in the European alps alone) ought to be studied in North America in connection with the *Boloria* "*pales*" *alascensis* Holl.

So for Europe the main result is a heavy decimation, and disappearance of many species which Europe formerly had in common with North America at the end of the pleistocene. But even in the post-pleistocene period the development of the fauna of Europe has taken a course different from that in North America. Here those regions that had become free from ice, were filled up again by the pre-glacial fauna which had deviated to the south. This fauna had preserved its basic stock, following successively the divers "life-zones". In Europe the re-colonisation issued partly from the places of refuge in the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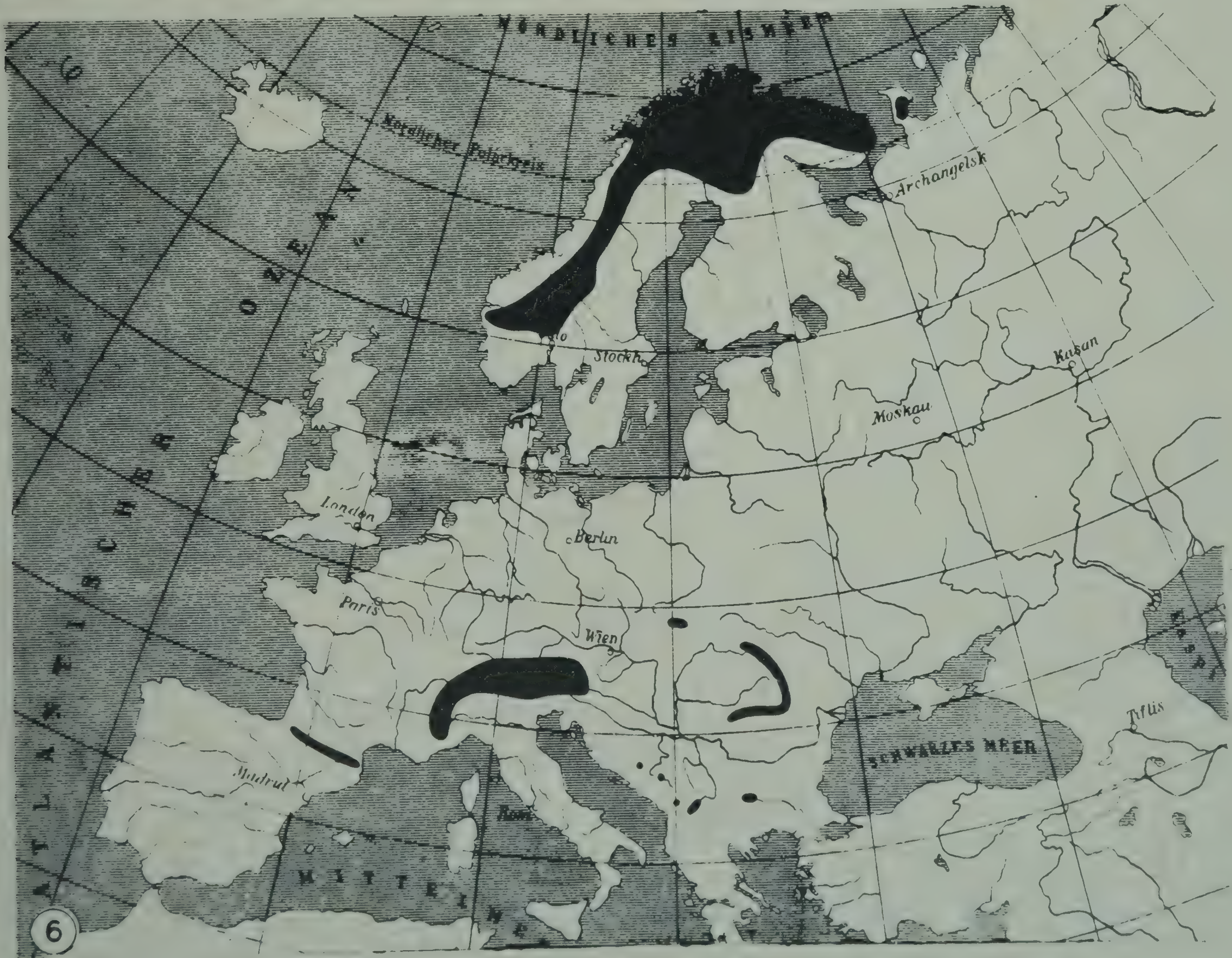
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Fig. 5. Maximum glaciation of Europe, Riss glaciation (Holdhaus).

Fig. 6. Distribution of *Erebia lappona* Esp. (Holdhaus—Warnecke).

southern part of the continent (the northern timber-line was south of the Alps), and partly from new immigrants (possibly only re-immigrants) from the south east and especially from the east (Siberia). Certainly most of the Siberian species are post-glacial ones, and this deduction is drawn from the fact that most of them are missing in the European refuges, and that in regard to their racial development they differ very little from the Asiatic forms.

But even the immigration to Europe from the east and southeast has not been able to compensate for the enormous decimation of the pre-glacial fauna. The European fauna of Lepidoptera has remained a poor, scanty one.

In addition, and in a decided way, the different directions of the high mountains of Europe and those of North America, have had an enormous effect on the fauna also in the post-glacial period. While causing a decimation of the fauna in the pleistocene, this situation brought about a far-reaching disjunction among many varieties in the post-glacial period. Let me only refer to one such type of extension that cannot be duplicated in kind or extent in North America, but which is especially characteristic for Europe. That is the boreo-alpine type of distribution. Boreo-alpine species of animals are those which occur, in a discontinuous range in the north of Europe and in the higher regions of the mid-European (partly south European) mountains, whereas they are totally, or near totally, absent from the middle-regions (Holdhaus, 1954). This type of range, as I emphasized, is impressively confined to Europe. The boreo-alpine species, however, are not endemic in Europe. In the north we come across many boreo-alpine species in Siberia, as far up as to the Altai and Mongolia, and some are also circumpolar.

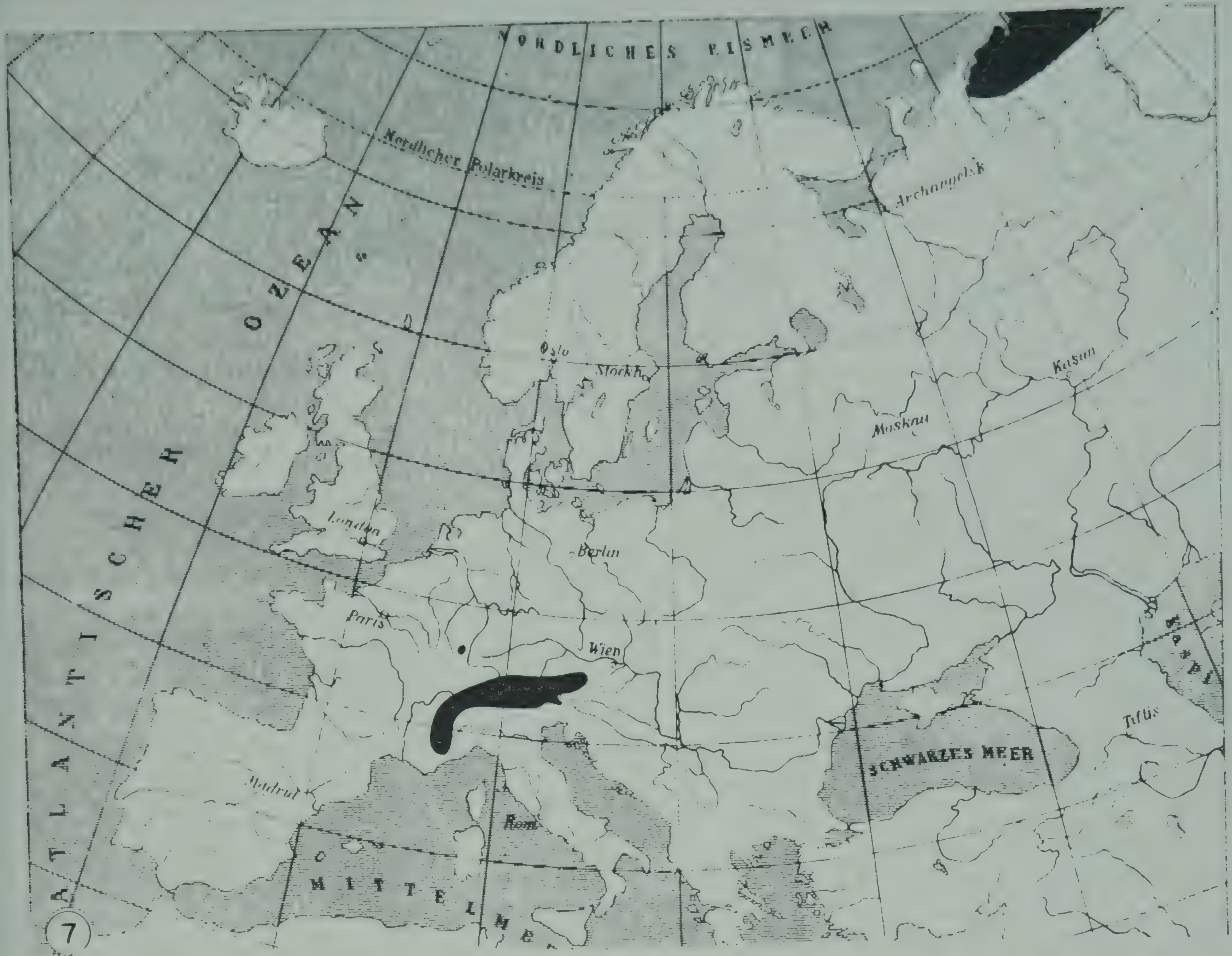
First let me give as example the distribution of the butterfly *Erebia lappona* Esp. (Fig. 6). During the glacial periods such species lived in the ice-free tundra regions of mid-Europe between the southern borders of the northern ice-cap and the northern border of the glaciers of the high mountains which had advanced far into their respective fore-lands. Hence they are species adapted to the climate of their time. As the ice retreated some specimens of a same species followed the receding ice northwards, while other specimens of the same species moved southwards to the high mountains. The intermediate zone no longer served the ecological requirements of the species, and became deserted. The results were disjunctions of 1,000 kilometres in Europe, which are far less extensive than those in North America.

It has to be noted that part of these species have become stationary in several suitable places of the interzone touched during their retreat. Such relicts are found in the upper layers of some uplands, mires and bogs. It would be surprising if this were not so. Nevertheless the centres of boreo-alpine distribution are in the southern high mountains, and in Fennoscandia.

There are about 200 species of boreo-alpine animals. One of them is the snow-hare (*Lepus variabilis* Pall.), and I leave it open to discussion whether those occurring in Greenland and North America can be regarded as separate species or not. As to birds, there are two boreo-alpine species, the rock ptarmigan, (*Lagopus mutus* Mont.) and the three-toed woodpecker (*Picoides tridactylus* L.). The northern and southern representatives of these groups never meet. In relation to their large number, it is mostly insects that are represented among the boreo-alpine species. According to Holdhaus (1951) the following figures are taken into consideration. They are species which are boreo-alpine in a strict sense:—Odonata: 2; Orthoptera: 2; Coleoptera: 43; Hymenoptera: 3; Diptera: 55; Lepidoptera: 33 (so-called Macros), 22 (so-called Micros).

The provenance of these species is highly instructive and gives proof of the above mentioned origin of the boreo-alpine type of distribution. It is not uniform. Among them there are arctic species, that means species which chiefly live far in the north, furthermore alpine species, namely species of the European and other high mountains, and even species of the Asiatic high steppes.

Of arctic descent there are for instance the snow-hare and the two birds, and there are of arctic descent also the holarctically distributed species of insects as:—*Aeschna coerulea* Ström (Ander, 1950), *Aeropedellus variegatus* F.W., *Podisma frigida* Boh., *Corymbites rugosus* Gyllh. (Fig. 7), *Phytodecta affinis* Gyllh. (Fig. 8), *Bombus lapponicus* F., *Agrotis speciosa* Hb., *Anarta melanopa* Hb., *Plusia hochenwarthi* Hoch., *Larentia munitata* Hb., *Fidonia carbonaria* Cl., and *Arctia quenselii* Payk. (Fig. 10).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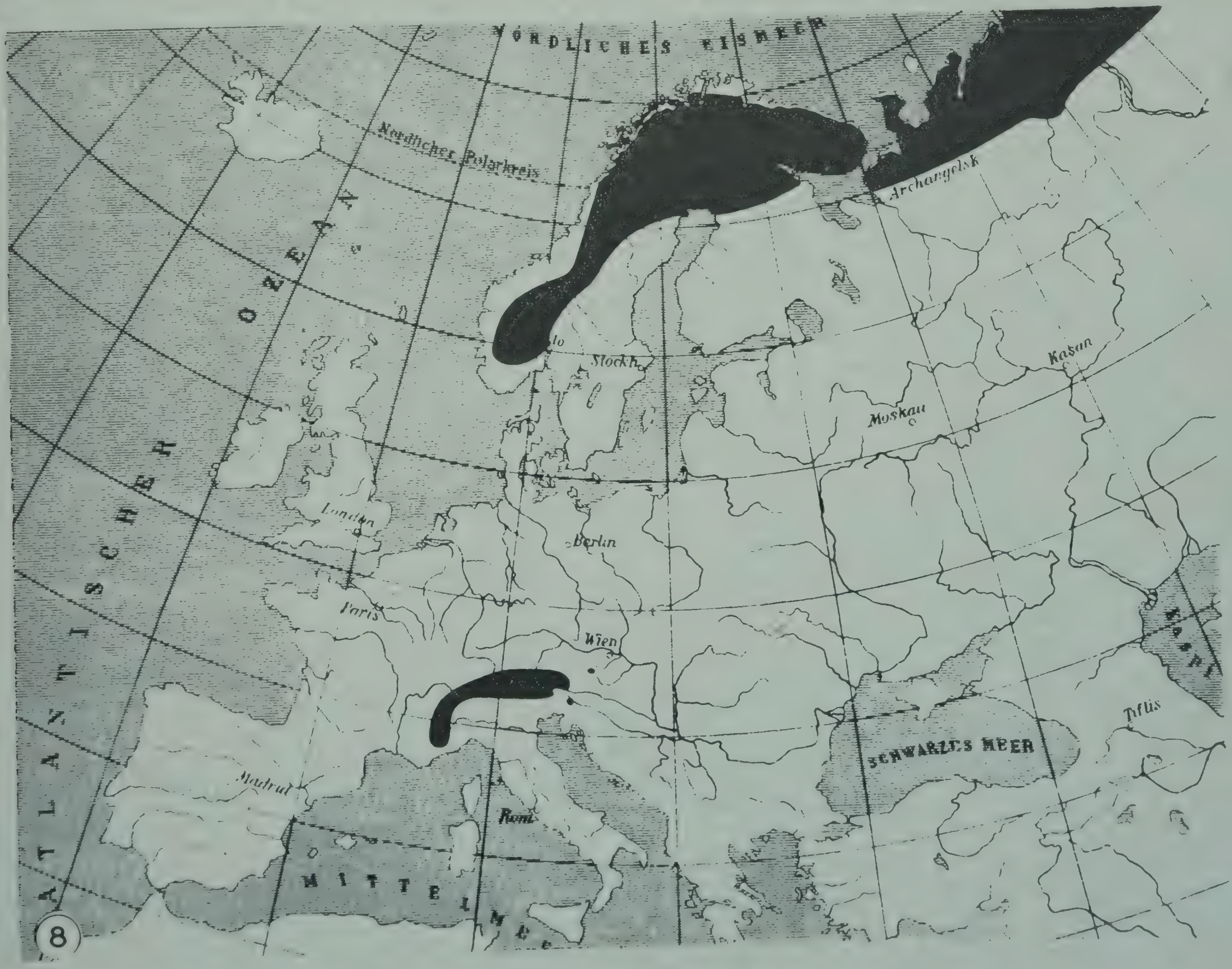
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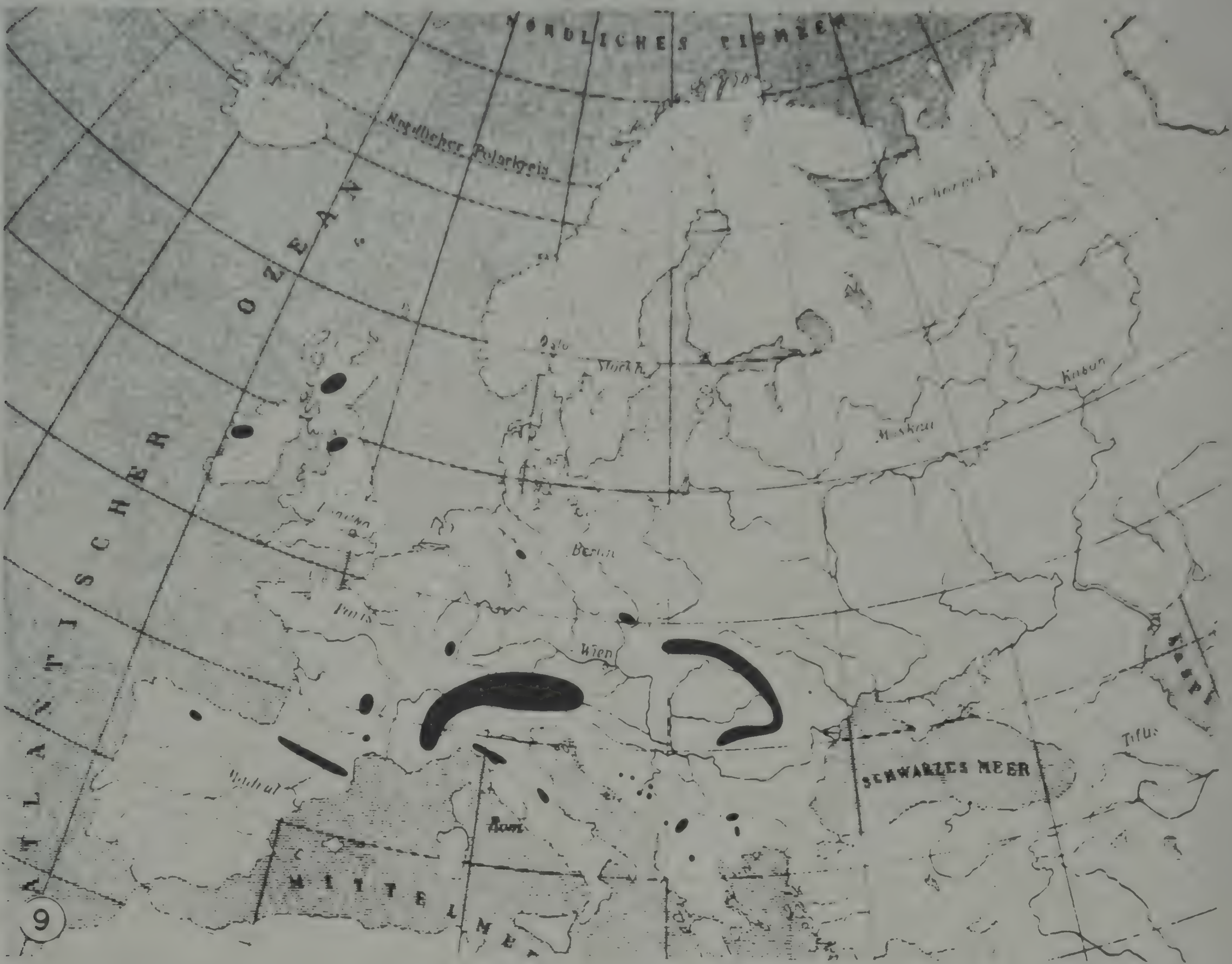
Fig. 7. Distribution of *Corymbites rugosus* Germ. (Holdhaus).

Fig. 8. Distribution of *Phytodecta affinis* Gyllh. (Holdhaus).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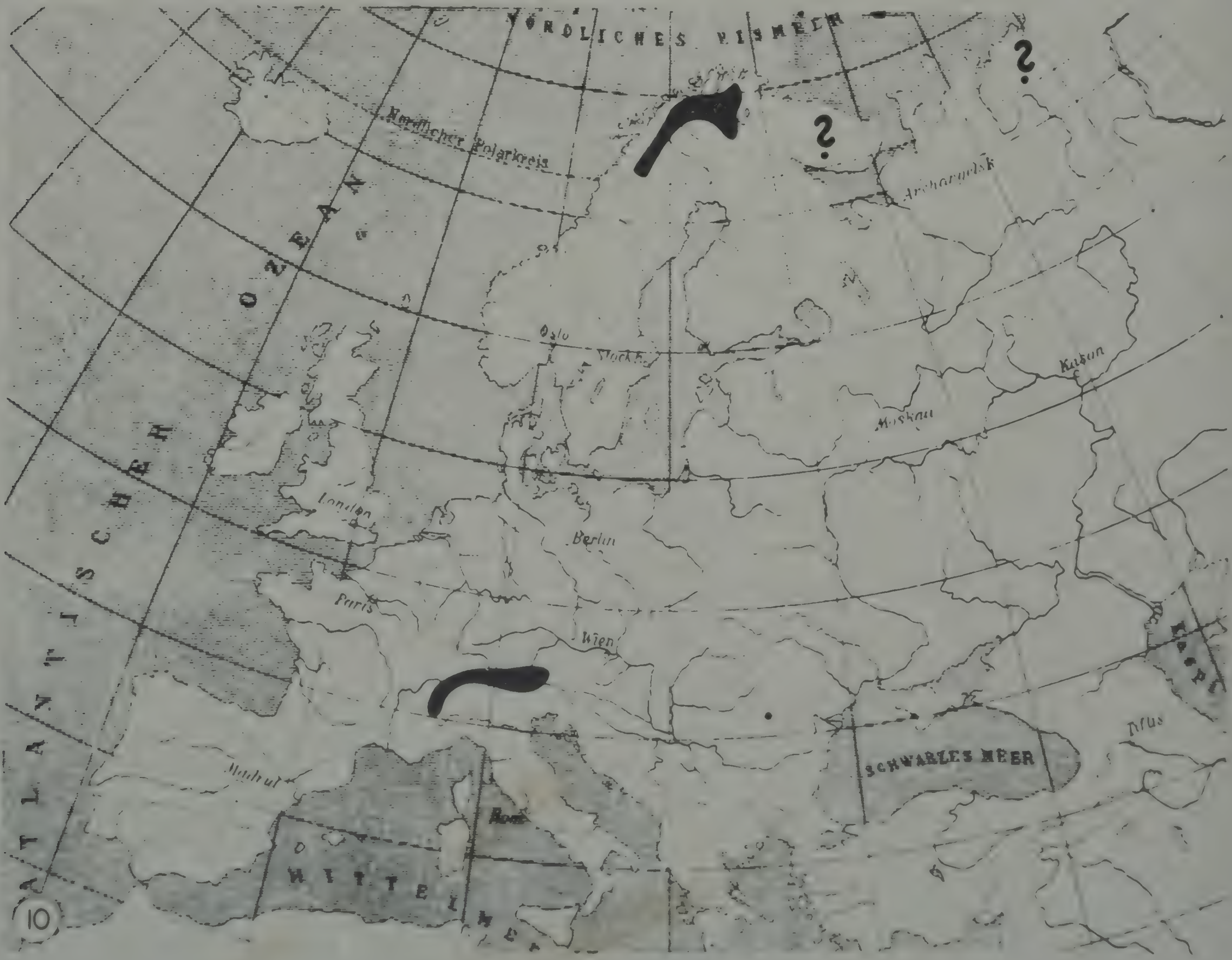
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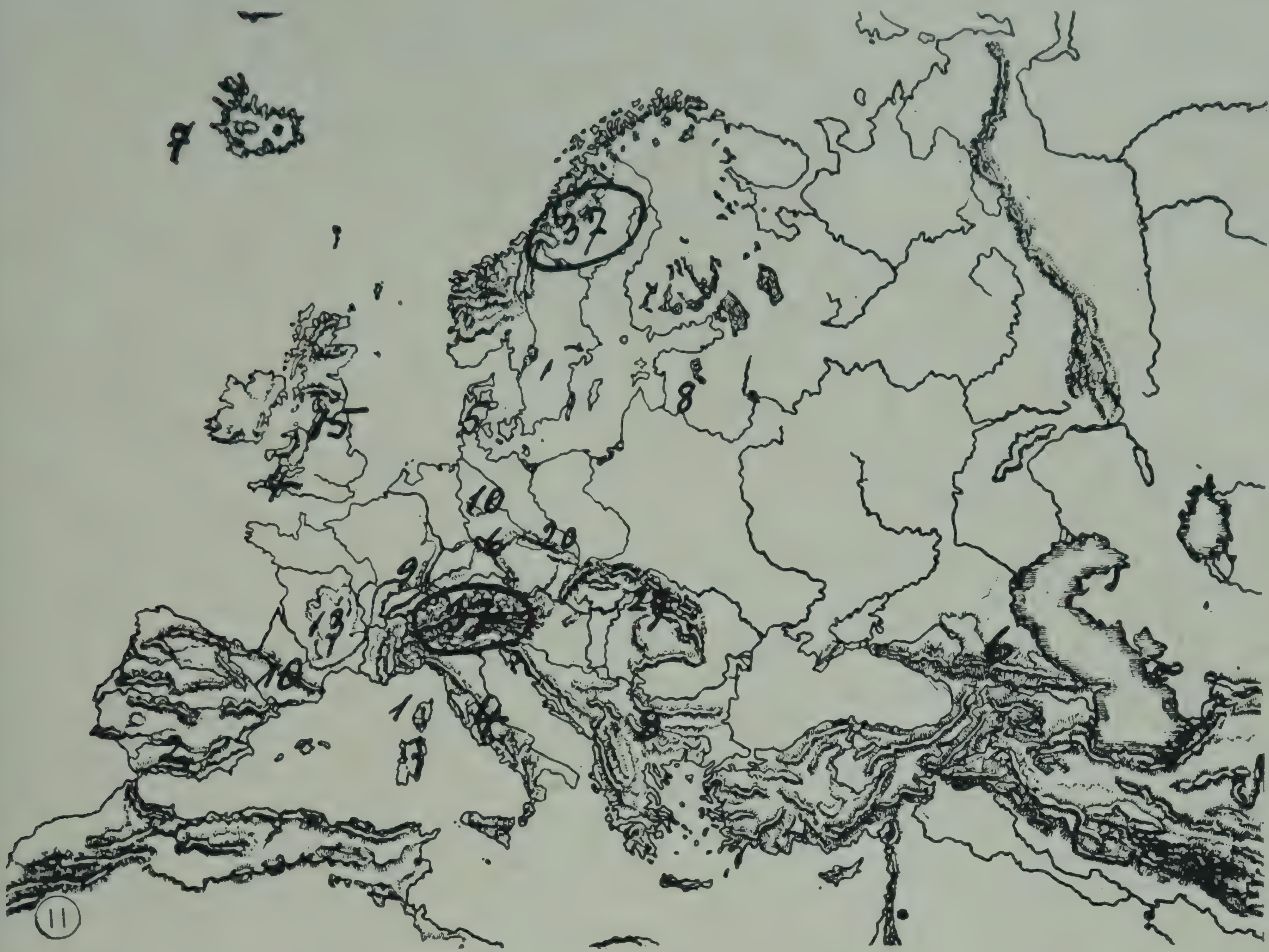
Fig. 9. Distribution of *Erebia epiphron* Knoch. (Holdhaus—Warnecke).

Fig. 10. Distribution of *Arctia (Orodemnias) quenselii* Payk. (Holdhaus—Warnecke).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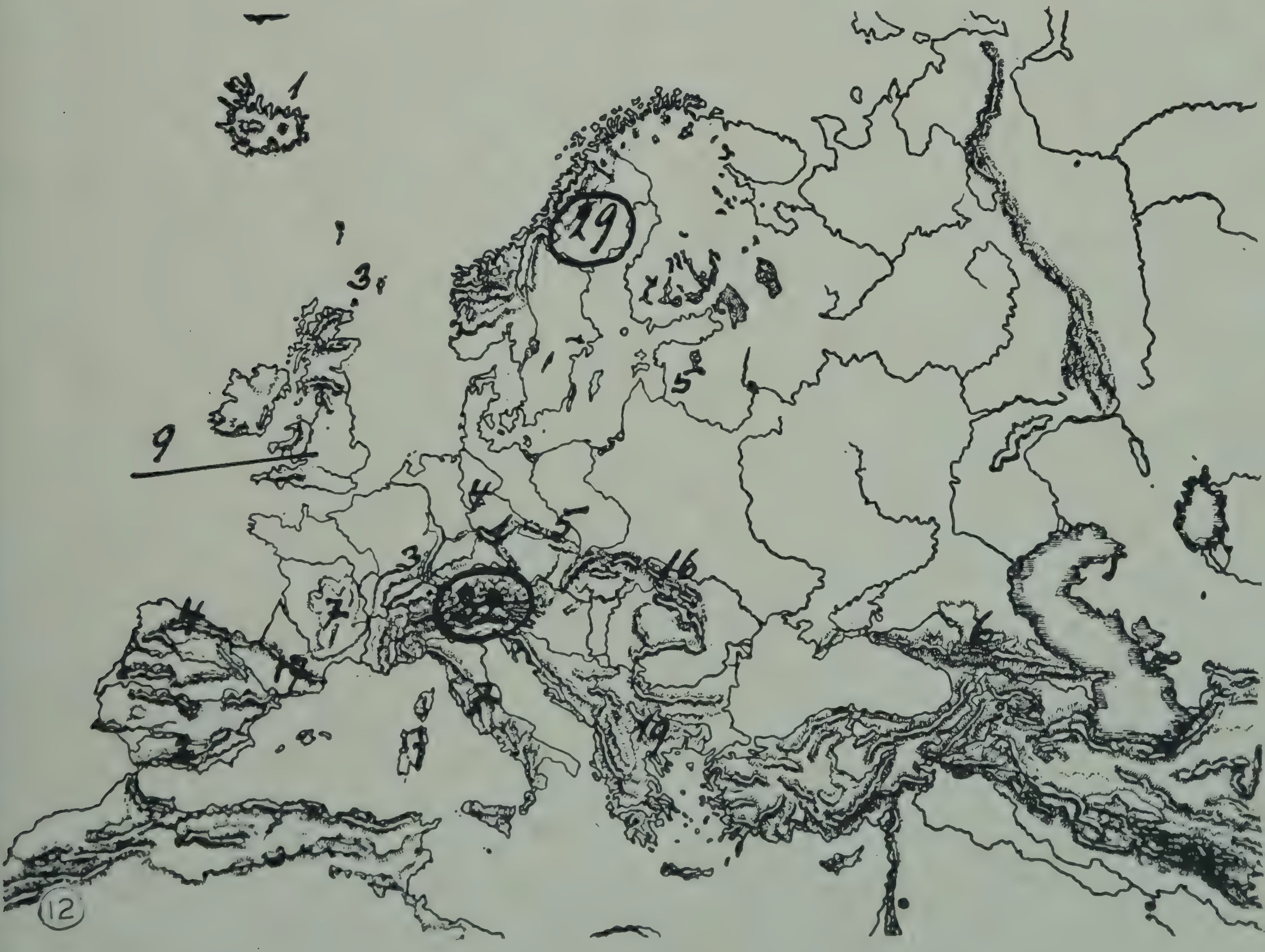
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Fig. 11. Distribution of the boreo-alpine Coleoptera.

Fig. 12. Distribution of the boreo-alpine Lepidoptera.

Of alpine descent, however, are:—*Pterostichus kokeili* Mill., *Geodromicus globulicollis* Mannh., *Helophorus glacialis* Vill., *Parnassius phoebus* F., *Pieris callidice* Esp., *Erebia epiphron* Knoch. (Fig. 9), *Hadena maillardi* H.-G., and *Zygaena exulans* Hoch.

As inhabitants of the Asiatic steppes the following may be characterised:—*Erebia lappona* Esp., and *Arctia flavia* Fuessl.

Thus it follows that the boreo-alpine species represent a mixture of the most diverse fauna elements. This mixing has been made less difficult by the repeated change in advancing and retreating during the separate stages of the glacial period.

There is an opinion that this type of distribution of the boreo-alpine species did not develop during the pleistocene, but much earlier in the pre-tertiary. But this supposition of a tertiary evolution of the boreo-alpine type may be decisively refuted by the following fact:—The high mountain ranges of the Kaukasus, including Armenia and the Balkan which lie along these tracks, show partly fewer boreo-alpine species than the summits of the uplands which were situated directly on the southern border of the northern inland-ice, as for instance the Harz Mountains and the Sudetes (Fig. 11, the boreo-alpine Coleoptera; Fig. 12, the boreo-alpine Lepidoptera).

There is no need to waste words on the fact that these boreo-alpine disjunctions cannot have originated in the post-glacial period, that means to say independent of the retreating glaciation. It is true, however, that we know of such disjunctions that have developed during the last post-glacial period in Europe, which show a distant likeness and, hence, in former times were frequently confused with the boreo-alpine disjunctions, although, actually, what we find here are in many cases lately immigrated "Siberian" species of the post-glacial period which subsequently have retreated once again (Warnecke, 1954).

Whether in Siberia we meet with a same or either a similar phenomenon, this question cannot be answered with certainty yet owing to the still incomplete investigation of Asia, although it may hardly be assumed that the conditions over there in the pleistocene period were completely different ones. Up to the 60th northern latitude Siberia is said to have been covered by an only slightly changing layer of granulated snow (firn), although, as a matter of fact, the high mountains of central Asia and western Siberia have developed gigantic glaciers.

As far as North America is concerned, there seems to have been but a simple falling back, as regards the disjunctive areas, a staying behind during the retreat to the north. Some northern species common in the White Mountains in New Hampshire, namely the Lepidoptera *Anarta melanopa* Thnbg., *Plusia hochenwarthi* Hoch., and the Odonata *Aeschna coerulea* Ström may be regarded as relicts in this sense.

However, for North America another disjunction, also reaching back to the pleistocene, seems to be of far greater importance. In Europe there is no similar parallel like this north-south divide separating an Atlantic from a Pacific fauna region, caused by both the north-south course of the Rocky Mountains and the middle arid zones.

The summary of my statements is thus: In comparison with North America it is not the simple "staying behind" of northern species far in the south that is characteristic for Europe, but the exchange of cold-adapted species between the north and the south, thus the shifting of arctic species to the southern high mountains and of southern alpine species in the high arctic and in this way the great mixture of different fauna elements in Europe.

REFERENCES

Ander, Kjell. 1950. Zur Verbreitung und Phänologie der boreoalpinen Odonaten der Westpalaearktis. *Opusc. Entom.* 15: 53–71.

Clark, A. H. 1932. The butterflies of the District of Columbia and vicinity. *Smithsonian Institution Bull.* 157.

Dillon, L. S. 1956. Wisconsin climate and life zones in North America. *Science* 123(3188): 167–174.

Klots, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Cambridge, Mass., *Riverside Press.*

Lindroth, Carl H. 1931. Die Insektenfauna Islands und ihre Probleme. *Zoologiska bidrag fran Uppsala* 13: 105–599.

Reinig, W. F. 1937. Die Holarktis. Jena.

Rensch, B. 1952. Verteilung der Tierwelt im Raum. *In* Handbuch der Biologie, 1. Teil. Ak. Verlagsgesellschaft, *Athenaion*, Potsdam.

Walter, H. 1954. Einführung in die Phytologie. III. Grundlagen der Pflanzenverbreitung. Einführung in die Pflanzengeographie. Zweiter Teil. Arealkunde. Verlag *Eugen Ulmet*, Stuttgart.

Warnecke, G. 1954. Über postglaziale Arealdisjunktionen europäischer Makrolepidopteren. *Deutscher Entomologentag in Hamburg*, 30. 7. bis 3. 8. 1953: 33–47.

Warnecke, G. and K. Holdhaus. 1954. Lepidoptera, Schmetterlinge. *In* Holdhaus, K.: Die Spuren der Eiszeit in der Tierwelt Europas. Universitätsverlag *Wagner*, Innsbruck, pp. 378–413. t. 46–52.

Zoogeographische Betrachtungen zur Rhopaloceren-Fauna Mitteleuropas (Lepidoptera)

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ZUSAMMENFASSUNG

Die 230 in Mitteleuropa vorkommenden Rhopalocera *wurden nach eingehenden Studien ihres rezenten Gesamtareals in 12 Verbreitungstypen aufgegliedert und ihre prozentualen Anteile ermittelt: boreoaltaisch-alpin 12 Arten = 5,2%, altaisch-alpin 37 Arten = 16%, europäisch 4 Arten = 1,7%, holomediterran 8 Arten = 3,5%, atlanto-mediterran 6 Arten = 2,6%, pontomediterran 8 Arten = 3,5%, euromediterran-vorderasiatisch 27 Arten = 11,7%, europäisch-vorderasiatisch 14 Arten = 6,1%, europäisch-westasiatisch 13 Arten = 5,6%, euroasiatisch 59 Arten = 25,6%, paläarktisch (holarktisch) 27 Arten = 11,7% und ± paläarktisch 10 Arten = 4,3%, circumpolar 6 Arten = 2,6%. Mit Hilfe der Refugialtheorie wurde versucht, ihre vermutlichen Ausstrahlungsgebiete und die postglazialen Einwanderungen nachzuweisen. Ferner wurde die gegenwärtige Verbreitung in Mitteleuropa behandelt und die für die einzelnen Faunenelemente typischen Arealgrenzen in diesem Gebiet aufgezeigt.*

Mitteleuropa, wir verstehen darunter das Gebiet zwischen 6°—22° östlicher Länge und 46°—56° nördlicher Breite, ist Schnitt- und Endpunkt einer grossen Zahl von Faunenelementen wie kaum ein anderes Gebiet der europäischen Subregion. Bereits in früherer Zeit ist verschiedentlich der Versuch unternommen worden, die Lepidopteren des mitteleuropäischen Faunenbereiches zoogeographisch zu analysieren (Hofman, Pabst, Rebel, Zerny, Hormuzaki, Caradja etc.). Diese Arbeiten sind heute jedoch in vielen Punkten überholt, da sich vor allem in den letzten zwei Jahrzehnten nicht nur eine neue, sowohl die ökologische als auch die historische Seite berücksichtigende, Betrachtungsweise zoogeographischer Probleme herausgebildet hat, sondern auch unsere Kenntnisse über die Gesamtverbreitung vieler Arten wesentlich erweitert wurde. Hinzu kommt die Refugialtheorie, mit deren Hilfe heute viele Fragen der Verbreitung und Ausbreitung zu deuten sind, die vorher nicht zu erklären waren. In jüngster Zeit haben sich besonders de Lattin, Reinig und Warnecke um die Lösung verschiedener lepidopterologisch-zoogeographischer Probleme verdient gemacht.

Es soll nun der Versuch unternommen werden, für eine Gruppe der Lepidopteren eine dem gegenwärtigen Stand unserer Kenntnisse entsprechende zoogeographische Analyse zu geben, und zwar für die in dieser Hinsicht am besten durchforschten Rhopalocera. In Anbetracht der gebotenen Kürze kann dies natürlich nur ein allgemeiner Überblick sein. Es kommt mir hier besonders darauf an aufzuzeigen, welche Verbreitungstypen bezw. Faunenelemente sich an der Zusammensetzung der mitteleuropäischen Rhopaloceren-Fauna beteiligen, welche als ihre Herkunfts- und Ausstrahlungsgebiete angesehen werden können, sowie ihre prozentualen Anteile zu ermitteln. Weiterhin soll untersucht werden, ob Beziehungen zwischen den einzelnen Verbreitungstypen und den speziell in Mitteleuropa verlaufenden Arealgrenzen bestehen.

Praeglaziale Formen aus der Tertiärzeit, wie sie sich beispielsweise noch heute als Relikte in Südeuropa erhalten haben, sind in Mitteleuropa nicht mehr anzutreffen. Diese sind entweder infolge der enormen Klimaverschlechterungen ausgestorben oder abgedrängt worden. Die ältesten Bestandteile unserer rezenten Fauna sind eine Gruppe von Arten, deren Einwanderung in den mitteleuropäischen Raum zeitlich mit dem Beginn der Eiszeit zusammenfällt. Sie kamen mit der von Nordeuropa ausgehenden Vereisung aus den Tundrengebieten des hohen Nordens in unsere Breiten und fanden während des Eiszeitalters zwischen dem Südrand der nordischen Eismassen und der Alpenvergletscherung, d.h. in dem Gebiet zwischen den deutschen Mittelgebirgen und der Donau, das man sich zu dieser Zeit als baumlose Tundra vorzustellen hat, zusagende Lebensbedingungen. Mit dem Rückgang der Vereisung und der einsetzenden Erwärmung zogen sich einige Arten sowohl in die höheren Lagen der Gebirge als auch am Rande der abziehenden Gletschermassen nach Norden zurück. Andere Arten waren scheinbar nur imstande, eine der beiden Rückzugsmöglichkeiten auszunutzen. Dieser Prozess hat sich nicht nur in Europa, wie vielfach angenommen wird, sondern auch in Asien und Nordamerika abgespielt. Hieraus ergeben sich zoogeographisch drei Verbreitungstypen, für Mitteleuropa die beiden folgenden:

Boreo-altaisch-alpiner Verbreitungstyp

12 Arten = 5,2%: *Parnassius phoebus* F., *Synchloe callidice* Esp., *Erebia euryale* Esp., *E. epiphron* Knoch, *E. pandrose* Bkh., *Proclossiana eunomia* Esp., *Clossiana thore* Hbn., *Boloria pales* Schiff., *Aricia nicias* Meig., *Agriades glandon* Prun., *Albulina orbitulus* Prun., *Pyrgus andromedae* Wallgr.

Das sind Arten, die in diskontinuierlicher Verbreitung heute sowohl in der nördlichen Paläarktis als auch in den Hochlagen der eurasiatischen Gebirge vorkommen, im Zwischengebiet dagegen in der Regel fehlen. Sie haben z.T. in ihrem Nord- bezw. Südareal verschiedene geographische Rassen gebildet. Einige sind circumpolar verbreitet. Nach Warnecke (in Holdhaus, 1954) sind von den dort insgesamt 33 aufgeführten Makrolepidopteren 9 Rhopaloceren hier oben aufgezählt, denen ich weitere 3 (*euryale*, *eunomia*, *nicias*) hinzugefügt habe. Sämtliche 12 Arten bewohnen das Alpengebiet, 7 beschränken ihr mitteleuropäisches Vorkommen auf diesen Raum. Von den restlichen 5 Arten finden sich 4 in der Tatra und den Karpaten, 2 in den Sudeten, und eine findet sich in den Vogesen, in der Eifel, Rhön und im Harz. Sie bewohnen Höhenlagen ab 800 m, z.T. aber erst ab 1500 bis 3000 m. *Eunomia* dehnt ihr Nordareal bis in die norddeutschen Ostseeküsten-Bezirke aus, d.h. sie fliegt dort in der Ebene.

Altaisch-alpiner Verbreitungstyp

37 Arten = 16%: *Pieris bryoniae* O., *Anthocaris euphenoides* Stgr., *Colias phicomone* Esp., *Erebia eriphyle* Frr., *E. manto* Esp., *E. claudina* Bkh., *E. flavofasciata* Heyne, *E. christi* Rätz., *E. pharte* Hbn., *E. melampus* Fuessl., *E. sudetica* Stgr., *E. triarius* Prun., *E. alberganus* Prun., *E. pluto* Prun., *E. gorge* Hbn., *E. mnestra* Hbn., *E. ottomana* H. Sch., *E. tyndarus* Esp., *E. cassioides* R. & Hochenw., *E. pronoe* Esp., *E. styx* Frr., *E. stirius* God., *E. montanus* Prun., *E. oeme* Hbn., *E. meolans* Prun., *Oeneis aello* Hbn., *Coenonympha satyrion* Esp., *Euphydryas ichnea wolfensbergeri* Frey, *E. cynthia* Hbn., *E. glaciegenita* Vrty., *Melitaea varia* H. Sch., *M. asteria* Frr., *Boloria napaea* Hffmgg., *Maculinea rebeli* Hirschke, *Polyommatus eros* O., *Pyrgus cacaliae* Rbr., *P. carlinae* Rbr.

Ihre Verbreitung erstreckt sich auf die Alpiden (Alpen, Pyrenäen, Apennin, Karpaten etc.) und Altaiden (Altai, Tienschan, Ural etc.), sie fehlen jedoch—im Gegensatz zu den Vorhergenannten—dem Norden Europas und Asiens. Einige scheinen überhaupt nur auf den Alpenraum beschränkt zu sein, z.B. *christi* und *flavofasciata* (Endemismen). Sämtliche 37 Arten finden sich in den Alpen, 9 in den Karpaten, jeweils 4 in der Tatra, im Schweizer Jura und in den Vogesen, 2 in den Sudeten und jeweils 1 Art findet sich noch im Schwarzwald und im Thüringer Wald.

Diesen 49 Arten stehen 181 gegenüber, die man nach ihrem allgemeinen Lebensraum als arboreale (Wald-) Elemente zusammenfassen kann. Letztere können auf Grund ihrer klimatisch-ökologischen Ansprüche erst postglazial in unseren Raum eingewandert sein. Als Ausbreitungszentren müssen die Eiszeitrefugien angesehen werden. Zwischen diesen und den rezenten Verbreitungsbildern besteht ein direkter ursächlicher Zusammenhang, und zwar entspricht einem jeden eiszeitlichen Refugialgebiet in der Holarktis ein bestimmter Verbreitungstyp, der seine Ursache eben in der Ausstrahlung von diesen Gebieten aus hat (de Lattin, 1951). Eine grosse Zahl solcher Refugialgebiete ist in den letzten Jahren besonders durch Reinig und de Lattin bekannt und lokalisiert worden. Es besteht also die Möglichkeit, vom rezenten Gesamtareal einer Art oder einer Gruppe von Arten mit identischer Verbreitung, Rückschlüsse auf ihre Herkunft und Ausstrahlungsgebiete zu ziehen.

Behandeln wir zunächst die Faunenelemente, die aus dem mediterranen Grossrefugium bis nach Mitteleuropa ausgestrahlt sind. Nach ihrem rezenten Gesamtareal lassen sie sich wie folgt klassifizieren.

Europäischer Verbreitungstyp

4 Arten = 1,7%: *Melitaea parthenoides* Kef., *Nemeobius lucina* L., *Everes alcetas* Hffmgg., *Spialia sertorius* Hffmgg.

Diese 4 Arten sind aus den Mediterran-Refugien der Balkan-, Apennin- und der Iberischen Halbinsel, wo sie auch heute noch ihre maximale Ausbreitung haben, bis nach Mitteleuropa—*lucina* sogar bis Südengland und Südschweden—vorgedrungen. Während das Areal von *parthenoides* und *sertorius* z.T. bis an den Rand der deutschen Mittelgebirge reicht, findet *alcetas* bereits in den Südtälern der Alpen und in Nieder-Österreich ihre Nordgrenze.

Holomediterraner Verbreitungstyp

8 Arten = 3,5%: *Gonepteryx cleopatra* L., *Colias australis* Vrty., *Hyponephele lupinus* Costa, *Pyronia cecilia* Vall., *Syntarucus pirithous* L., *Lysandra escheri* Hbn., *Reverdinus marrubii* Rbr., *Lavatheria lavatherae* Esp.

Ihr Areal deckt sich im wesentlichen mit dem Gebiet, dass wir heute als mediterranes Grossrefugium bezeichnen. Postglaziale Arealerweiterung hat bei diesen Arten nur in sehr geringem Masse stattgefunden. Ihre Nordgrenze verläuft von den Pyrenäen über Südfrankreich am Südrand der Alpen entlang nach Jugoslavien und Bulgarien. Nur *cecilia* und *lupinus* gehen auf der Balkanhalbinsel etwas nördlicher bis Rumänien bezw. Ungarn. Zwei Arten (*australis* und *pirithous*) wandern jahrweise in nördlichere Gebiete, ohne hier jedoch heimisch werden zu können. So wurde *pirithous* beispielsweise bei Bozen, Augsburg, Stuttgart, Basel etc. angetroffen. Die Wanderungen von *australis* scheinen regelmässiger zu erfolgen und die Falter weiter nach Norden vorzudringen. Neuerdings wurde die Art sogar in Thüringen festgestellt.

Atlanto-mediterraner Verbreitungstyp

6 Arten = 2,6%: *Hipparchia aelia* Hffmgg., *Melitaea deione* Hbn., *Philotes baton* Bergstr., *Pyrgus malvoides* Elw. & Edw., *P. onopordi* Rbr., *P. cirsii* Rbr.

Für diese Gruppe kommt als Ausstrahlungsgebiet nur der westliche Teil des mediterranen Grossrefugiums, den man als atlanto-mediterranes Sekundärrefugium bezeichnet, in Frage, d.h. geographisch das paläarktische Nordafrika (Marokko, Algerien, Tunesien), sowie die Iberische und Apennin-Halbinsel. Die Ausbreitungstendenz dieser westmediterranen Formen ist äusserst gering. Das Vorkommen in Mitteleuropa beschränkt sich bei 5 Arten auf die südlichsten bezw. südwestlichsten Teile (Schweiz, Südalpen; *cirsii* noch in Bayern, Fränkische Schweiz und Mainfranken, z.B. Nürnberg, Fürth, Ulm, Kreuznach bis Kissingen, ? Wien; *baton* bis Jena). Nur *aelia* geht nördlicher bis in die Ostsee-Provinzen. Die lokale Verbreitung von *aelia* in Mitteleuropa und vor allem das inselartige Vorkommen in Südnorwegen (ssp. *norwegica* Strand) deuten darauf hin, dass diese Art früher gleichmässiger und eventuell auch weiter verbreitet war. Nach den Lebensansprüchen des Falters ist zu vermuten, dass die Einwanderung in der postglazialen Wärmezeit erfolgt ist, zu der keine wesentlichen Unterschiede zwischen den Klimaten des Mittelmeer-Raums und Zentraleuropas bestanden haben werden. In dieser trocken-warmen Periode wird sicher ein weit grösserer Anteil mediterraner Elemente in Mitteleuropa eingewandert sein, als wir es heute noch feststellen können. Mit Einsetzen der feucht-kalten Witterung sind diese Arten dann wieder zurückgedrängt worden oder haben sich eben nur noch an engbegrenzten geeigneten Lokalitäten halten können, woraus dann jene zerrissene und inselartige Verbreitung hervorgeht. Es sind mehrere solcher Beispiele bekannt.

Ponto-mediterraner Verbreitungstyp

8 Arten = 3,5%: *Zerynthia hypsiphyle* Schulz., *Pieris manni* Mayer, *Polygonia egea* Cr., *Thersamonia thersamon* Esp., *Everes decolorata* Stgr., *Meleageria daphnis* Schiff., *Pyrgus sidae* Esp., *Spialia orbifer* Hbn.

Diese Arten haben ihr Verbreitungs- und Ausbreitungszentrum in den östlichen Mediterran-Gebieten, vor allem auf der Balkanhalbinsel und in Kleinasien, d.h. es handelt sich hier um Elemente des ponto-mediterranen Sekundärrefugiums. Einige expansionistische Arten sind westlich bis ins Rhonetal vorgedrungen, ganz vereinzelt sogar bis an den Rand der Pyrenäen. Ihre Arealgrenze geht von dort dann in der Regel weiter am Südrand der Alpen entlang, einige finden sich jedoch nördlich noch verschiedentlich in Nieder-Österreich, Mähren und Böhmen, was zweifellos auf eine Einwanderung durch das Donautal zurückzuführen ist. Die Gebirgszüge des Böhmer Waldes und des Oberpfälzer Waldes, des Erzgebirges und der Sudeten geboten ihrer weiteren Ausbreitung halt. Nur *daphnis* ist es gelungen, diese natürliche Grenze zu überschreiten und bis Sachsen, Thüringen und Bayern vorzudringen.

Wenden wir uns nun einer Gruppe von Arten zu, deren Hauptverbreitungsgebiet sich neben dem Mediterraneum hauptsächlich in Vorderasien erstreckt. Man kann sie als mediterran-vorderasiatisches Faunenelement zusammenfassen. Nach ihrem Vorkommen bezw. Fehlen in Nordafrika lassen sie sich in die beiden folgenden Verbreitungstypen aufgliedern:

Euromediterran-vorderasiatischer Verbreitungstyp

27 Arten = 11,7%: *Iphiclides podalirius* L., *Agapetes galathea* L., *Hipparchia semele* L., *H. statilinus* Hufn., *H. arethusa* Esp., *Chazara briseis* L., *Satyrus actaea* Esp., *Pararge aegeria* L., *Dira megera* L., *D. maera* L., *Maniola jurtina* L., *Pyronia tithonus* L., *Coenonympha pamphilus* L., *Melitaea cinxia* L., *Pandoriana maja* Cr., *Thecla quercus* L., *Strymon ilicis* Esp., *Heodes alciphron* Rott., *Jolana jolas* O., *Lysandra thersites* Cant.—Chapm., *L. argester* Bgstr., *L. bellargus* Rott., *Carcharodus alceae* Esp., *Reverdinus floccifera* Z., *Pyrgus armoricanus* Obth., *Adopaea silvester* Poda, *Thymelicus actaeon* Rott.

Diese Arten finden sich in Nordafrika—Im Gegensatz zu den rein holomediterranen Formen hat das euromediterran-vorderasiatische Faunenelement wesentlich mehr expansionistische Arten aufzuweisen, sie haben sich ausserdem weiter in Mitteleuropa und darüber hinaus teilweise bis Nordeuropa ausgebreitet. Durch den ganzen mitteleuropäischen Raum und weiter bis Süd- teilweise sogar bis Mittelskandinavien sind 11 Arten verbreitet; 9 finden an der Ostsee, 2 im Bereich der Mittelgebirge und 3 in Süddeutschland ihre Nordgrenze. Nur 2 Arten haben die Alpen nicht überschritten, wie dies für die vorher behandelten rein holomediterranen Faunenelemente typisch ist.

Europäisch-vorderasiatischer Verbreitungstyp

14 Arten = 6,1%: *Pieris ergane* Hbn. *Colias myrmidone* Esp., *Hipparchia fagi* Scop., *Brintesia circe* F., *Coenonympha arcania* L., *Limenitis anonyma* Lewis, *Melitaea britomarits* Assm., *Brenthis hecate* Esp., *Strymon acaciae* F., *Polyommatus eroides* Friv., *Lysandra coridon* Poda, *Agrodiaetus admetus* Esp., *A. ripartii* Frr., *A. damon* Schiff.

Fehlen in Nordafrika und teilweise bereits in Südwesteuropa—Ihre Verbreitung in Mitteleuropa erreicht nicht das Ausmass der vorigen Gruppe. 5 Arten finden schon im Bereich der Alpen und Karpaten ihre Nordgrenze oder sind höchstens durch das Donautal bis nach Nieder-Österreich und Mähren vorgedrungen; für weitere 4 bilden die Mittelgebirge die Arealgrenze, nur 3 vermochten bis in die Ostsee-Provinzen vorzudringen. Während alle bisher angeführten Arten eine in Ost—West—Richtung verlaufende Arealgrenze in Zentraleuropa aufzuweisen hatten (Nordgrenze), stossen wir bei 2 Arten auf den Typus einer ausgesprochenen Westgrenze: *myrmidone* und *eroides*. Sie erreichen mit ihren westlichsten Ausläufern nur das östliche Mitteleuropa und das östliche Mediterraneum. Da sie jedoch der südlichen Balkanhalbinsel, der europäischen Türkei und Nordwestbithynien fehlen, konnten sie sich nur auf dem Wege durch Südrussland bis hierher ausbreiten. Als Glazialrefugium dieser Arten kommt vor allem das Flach- und Hügelland Transkaukasiens in Frage, dem sich vermutlich das Südufer des Kaspischen Meeres und die Südküste der Krim angliedern. Sie können auch als kaspisches Faunenelement abgetrennt werden (de Lattin, 1951).

An den eben abgehandelten Verbreitungstypus schliesst sich eine Gruppe an, die zwischen diesem und dem euroasiatischen steht.

Europäisch-westasiatischer Verbreitungstyp

13 Arten = 5,6%: *Parnassius apollo* L., *P. mnemosyne* L., *Colias chrysotheme* Esp., *Satyrus ferula* F., *Melitaea trivia* Schiff., *Clossiana titania* Hbn., *Heodes tityrus* Poda, *Cupido sebrus* Hbn., *Philotes vicrama* Moore, *Maculinea alcon* Schiff., *M. nausithous* Bgstr., *Plebejus pylaon* F. W., *Pyrgus carthami* Hbn.

Das rezente Areal erstreckt sich über Vorder-, das westliche Zentral- und Nord-Asien (etwa bis zum Altai und Westsibirien) und in Europa vor allem auf die östlichen, südlichen und zentralen Teile. Als Refugien sind neben den bereits bekannten vorderasiatischen (Armenien, Transkaukasien, Elbrus) besonders auch ein Teil der zentral-asiatischen anzusehen (Himalaya, Kaschmir, Tienschan). *Apollo* und *mnemosyne* sind als montane Arten in Zentraleuropa auf die Hoch- und Mittelgebirge beschränkt. Sie fliegen jenseits der Ostsee auch in Südskandinavien; *tityrus* und *alcon* haben im Bereich der Ostsee ihre nördlichsten Vorkommen, *vicrama*, carthami und *titania* erreichen sie nur im Osten, letztere fehlt sonst aber wie *nausithous* der nördlichen Tiefebene. *Chrysotheme*, und *trivia* haben nur den südöstlichen und südlichsten Teil Mitteleuropas besiedelt (Tschechoslovakei, Nieder-Österreich, Ungarn, Südalpen). Während *chrysotheme* hier ihre äussersten nordwestlichen Arealausläufer hat, hat sich *trivia* weiter bis nach Spanien ausgebreitet. *Ferula*, *sebrus* und *pylaon*, die ebenfalls bis Spanien verbreitet sind, haben in den Südtälern der Alpen ihre Nordgrenze.

Euro-asiatischer Verbreitungstyp

59 Arten = 25, 6%: *Anthocaris cardamines* L., *Leptidea sinapis* L., *L. morsei* Fent., *Erebia ligea* L., *E. aethiops* Esp., *E. medusa* Schiff., *Minois dryas* Scop., *Aphantopus hyperantus* L., *Dira petropolitana* F., *Lopinga achine* Scop., *Coenonympha oedippus* F., *C. hero* L., *C. iphis* Schiff., *C. tullia* Muller, *Apatura iris* L., *A. ilia*

Schiff., *Limenitis camilla* L., *L. populi* L., *Neptis rivularis* Scop., *N. hylas* L., *Aglais urticae* L., *Inachis io* L., *Nymphalis xanthomelas* Esp., *Polygonia 1-album* Esp., *Araschnia levana* L., *Euphydryas maturna* L., *Melitaea diamina* Lang, *M. athalia* Rott., *M. parthenie* Bkh., *Mesoacidalia charlotta* Haw., *Fabriciana niobe* L., *Argyromone laodice* Pall., *Brenthis ino* Rott., *B. daphne* Schiff., *Clossiana selene* Schiff., *C. dia* L., *Boloria alethea* Hemming, *Thecla betulae* L., *Strymon spini* Schiff., *S. w-album* Knoch, *S. pruni* L.,*Heodes virgaureae* L., *Lycaena helle* Schiff., *Thersamonia dispar* Haw., *Palaeochrysophanus hippothoe* L., *Everes argiades* Pall., *Scolitantides orion* Pall., *Maculinea teleius* Bgstr., *M. arion* L., *Lycaeides idas* L., *L. argyrognomon* Bgstr., *Plebejus argus* L., *Aricia allous* Hbn., *Eumedonia chiron* Rott., *Erynnis tages* L., *Pyrgus malvae* L., *P. serratulae* Rbr., *Heteropterus morpheus* Pall., *Carterocephalus silvius* Knoch.

Als Eiszeitrefugien müssen wir für diese Gruppe neben den vorder- und zentralasiatischen Teilrefugien auch bezw. besonders, die ostasiatischen rechnen, denn ihr Gesamtareal erstreckt sich, von ganz wenigen Ausnahmen abgesehen, östlich bis zur pazifischen Küste. Als bekannte Ausstrahlungsgebiete sind hier die Küsten des Ochotskischen Meeres, das Mündungsgebiet des Amur, das Ussuri-Gebiet, Nord- und Mittelchina, die chinesisch-tibetanischen Grenzgebiete etc. (Reinig, 1950) zu nennen. Diese Faunenelemente sind in grosser Breite und Anzahl in nahezu alle Teile Europas eingewandert und bilden überall prozentual den grössten Anteil. 38 der 59 in Mitteleuropa vorkommenden euroasiatischen Rhopaloceren finden sich auch in Nordeuropa, wohin sie einmal über Mitteleuropa und die während der Ancyluszeit bestehende Landbrücke oder auf dem Wege über Nordrussland und Finnland gelangt sind. Diese 38 Arten sind mit Ausnahme der montanen und abgesehen von ganz wenigen, die in den stark vom Seeklima beeinflussten nordwestdeutschen Gebieten fehlen, ziemlich gleichmässig durch Mitteleuropa verbreitet. Einige erreichen hier ihre Westgrenze, z.B. *xanthomelas*, *laodice*, *silvius*. Bei 12 Arten verläuft die Arealgrenze an der Ostseeküste entlang. Auch fehlen diese in Nordwestdeutschland, so dass hier vom Typus einer Nordwestgrenze gesprochen werden kann. 7 Arten fehlen der norddeutschen Tiefebene völlig, sie finden sich südlich der Mittelgebirge vor allem in Schlesien, Böhmen, Mähren, Slovakei, Österreich, Ostalpen etc., *morsei*, *hylas* und *l-album* erreichen hier die nordwestlichsten oder überhaupt westlichsten Punkte ihres Gesamtareals.

Palaearktischer (holarktischer) Verbreitungstyp

27 Arten = 11, 7%: *Papilio machaon* L., *Aporia crataegi* L., *Pieris brassicae* L., *P. rapae* L., *P. napi* L., *Pontia daplidice* L., *Gonepteryx rhamni* L., *Hyponephele lycaon* Rott., *Vanessa atalanta* L., *V. cardui* L., *Nymphalis polychloros* L., *N. antiopa* L., *Polygonia c-album* L., *Euphydryas aurinia* Rott., *Fabriciana adippe* Rott., *Argynnis paphia* L., *Issoria lathonia* L., *Callophrys rubi* L., *Lycaena phlaeas* L., *Cupido minimus* Fuessl., *Celastrina argiolus* L., *Aricia agestis* Schiff., *Cyaniris semiargus* Rott., *Polyommatus icarus* Rott., *Adopaea lineola* O., *Ochlodes venata* Brem. & Grey, *Hesperia comma* L.

Das rezente Gesamtareal dieser Arten erstreckt sich über ganz Eurasien und Nordafrika, ausgenommen den hohen Norden, und greift bei 8 auch noch auf mehr oder weniger grosse Teile Nordamerikas über. Für sie können alle Glazialrefugien der Paläarktis (Holarktis) als Ausstrahlungsgebiete in Frage kommen. Sie sind ökologisch wenig anspruchsvoll, woraus sich ihre weite Verbreitung erklärt. Es ist ferner anzunehmen, dass sie sehr alte Arten sind und bereits praeglazial weit verbreitet waren.

Weitere 10 Arten = 4, 3%: *Euchloe ausonia* Hbn., *Colias hyale* L., *C. croceus* Fourc., *Melitaea phoebe* Schiff., *M. didyma* Esp., *Libythea celtis* Fuessl., *Lampides boeticus* L., *Glaucopsyche alexis* Poda, *Lysandra icarius* Esp., *Pyrgus alveus* Hbn. sind hier einzureihen.

Auch sie besiedeln grosse Teile Asiens, Europas und das paläarktische Nordafrika. Mit Ausnahme von *icarius*, deren Westgrenze durch unseren Raum geht, fehlen sie in Nordeuropa. *Phoebe*, *didyma*, *alexis* und *alveus* finden in Mitteleuropa ihre Nord- bezw. Nordwestgrenze. Während *hyale* und *croceus* nördlich der Alpen nur als Wanderfalter auftreten, haben *ausonia*, *celtis* und *boeticus* am Südrand der Alpen bereits ihre Nordgrenze.

Circumpolarer Verbreitungstyp

6 Arten = 2, 6%: *Colias palaeno* L., *Oeneis jutta* Hbn., *Clossiana euphrosyne* L., *Vacciniia optilete* Knoch, *Carterocephalus palaemon* Pall.

Obwohl auch sie in Eurasien und Nordamerika vorkommen, sollen sie hier gesondert aufgeführt werden; denn ihre rezente Verbreitung erstreckt sich nur auf die nördlichen Teile der Holarktis. Sie sind vor allem aus den Refugien der sibirisch-mongolischen Grenzgebirge, Nordchinas, der Amurmündung, des Ochotskischen Küstenstreifens und Südkamtschatkas ausgestrahlt. Sie bevorzugen sowohl in montanen Zonen wie auch in den Ebenen Moorbiotope. Daraus resultiert ihre teilweise lokale und inselartige Verbreitung, was oft zu Verwechselungen mit boreo-altaisch-alpinen Elementen geführt hat. Sie unterscheiden sich von diesen jedoch dadurch, dass sie auch in der Ebene vorkommen. Während *jutta* in Ostpreussen ihren südlichsten Arealausläufer hat, sind die anderen Arten bis in das Alpengebiet, *palaemon* und *euphrosyne* darüber hinaus noch weiter südlich verbreitet.

LITERATURVERZEICHNIS

de Lattin, G. 1949. Beiträge zur Zoogeographie des Mittelmeergebietes. *Verh. Deutsch. Zoologen*, Kiel. 1948: 143–151.

de Lattin, G. 1951. Über die zoogeographischen Verhältnisse Vorderasiens. *Verh. Deutsch. Zoologen*, Marburg. 1950: 206–214.

Forster, W., & Th. Wohlfahrt. 1952–1955. Die Schmetterlinge Mitteleuropas, II. *Franckh*, Stuttgart.

Friese, G. 1956. Die Rhopaloceren Nordostdeutschlands. *Beitr. Ent.* 6: 53–100, 403–442, 625–658.

Nordström, F. 1956. De fennoskandiska dagfjärilarnas utbredning. Lunds Univ. Årsskt. *Acta Univ. Lund.* (N.S.) 51 (1955), Nr. 1: 1–177.

Reinig, W. F. 1937. Die Holarktis. *Fischer*, Jena.

Reinig, W. F. 1950. Chorologische Voraussetzungen für die Analyse von Formenkreisen. Sylegomena Biologica, *Geest & Portig*, Leipzig, Ziemsen, Wittenberg: 346–378.

Seitz, A. 1909–1932. Die Gross-Schmetterlinge des Paläarktischen Faunengebietes m. Suppl. Stuttgart.

Warnecke, G., & K. Holdhaus. *In* Holdhaus, K. 1954. Die Spuren der Eiszeit in der Tierwelt Europas. *Abh. zool. bot. Ges. Wien* 18: 378–392.

The Northward Movement of Certain Species of European Lepidoptera and Its Relationship to Climatic Changes and Other Factors with Special Reference to the British Isles

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ABSTRACT

During the past twenty five years there appears to have been a distinct northward movement of a number of species of Lepidoptera, chiefly moths whose normal habitat is in the more southerly regions of Europe. Many of the species under review have recently become definite breeding residents and colonisers on the mainland of Great Britain where their presence may have previously been only sporadic. A distinction should be made between these species and those that are recognised as regular migrants from the Mediterranean and North Africa.

A similar and parallel movement of most of these species has been going on in other parts of Europe, notably in Denmark. The possible relationship of this northward trend and apparent recent climatic changes is discussed in the light of the fact that it has also been observed in both birds and fish.

Some twenty species of Lepidoptera falling into the category will be treated and described.

During the present century there has apparently taken place some very interesting changes in the status of several species of European Lepidoptera. It has, however, been during the past twenty five years that these changes and movements have been most marked and important. They have been most noticeable in the British Isles and other European countries of similar latitude. Those who study the Lepidoptera are familiar with certain species which are regular migrants in a general northerly direction across Europe, as for example the well-known Hawk-moths *Acherontia atropos* Linn., *Herse convolvuli* Linn., *Celerio livornica* Esp., and such common Noctuids as *Plusia gamma* Linn. There are others which have apparently a distinctly western line of migration such as *Leucania unipuncta* Haworth, *Plusia ni* Hübn. and *Rhodometra sacraria* Linn. All these insects appear sporadically in Northern Europe where they may breed for a single season and then die out to be replenished by a further immigrations some years later. There are also the occasional vagrants which reach the British shores from long distances as for instance *Plusia acuta* Walker, an inhabitant of tropical Africa which was recorded in England in 1955, probably borne by high air currents.

The species to be treated are those which have appeared chiefly in Great Britain and its neighbouring countries in recent years as entirely new colonisers or those for which there is evidence that they are likely to be breeding in these more northerly latitudes where they had been previously unknown in modern times.

There seems to be in nearly every instance a parallel movement northwards of the species under review, affecting the British Isles, Holland and Denmark alike. I am especially indebted to Dr. Skat Hoffmeyer of Aarhus and to Mr. Lempke of Amsterdam for most helpful and valuable records from their countries.

Naturally various theories have been put forward for the steady extension of range northwards not only of some of the Lepidoptera, but also of other Orders of insects as well as of certain birds and fish. A great deal of research has taken place into the climatic conditions of Northern Europe in recent times and particularly of the past few decades. Much work has been carried out in this field by Professor Gordon Manley of London, a noted pioneer and authority on this subject. In an illuminating lecture in 1944 he makes the following important pronouncement–:

"The Norwegian Glaciers reached their maximum in historic times about 1750. There were other advances in 1810 and about 1890. Since 1930 the melting away of the mountain snowfields has never since Roman times been so extensive as now." Again at the Meteorological Congress in Toronto in 1953 the same author says "I assume we are familiar with the very decided evidence of climatic amelioration round the North Atlantic since 1925. It has been shown by the retreat of the glaciers, the northward spread of warm Atlantic water and the increased growth of trees in Northern Scandinavia."

Both these statements are most significant since it was in the late 1920's that this movement of Lepidoptera towards the North began to be most marked. The other evidence to support the theory of the warming-up of the climate in Northern Europe is that since 1921 the coal-mining season in Spitzbergen has been doubled, from 95 days in 1909 to 175 days from 1930 to 1938. The mean rise of temperature in London from 1901 to 1930 has been 0.14°C, while in Northern Sweden it has been as much as 0.6°C during that period.

These facts and figures afford ample evidence in support of the theory that this apparent movement towards the North of Lepidoptera and other creatures is most probably associated with the warming-up of the climate in these more northerly latitudes of Europe, especially as some of the species of Lepidoptera are of distinctly Mediterranean origin and habitat.

With these introductory remarks I will say something about each of the species of Lepidoptera that fall into the category under review. They are divided into two groups, those which have become definitely new colonisers in recent years and those which appear to be in the process of doing so.

GROUP I

Species that have become new colonisers in recent years.

(a) THOSE WITH A WESTERLY TENDENCY

Leucania l-album Linn. This noctuid moth was of of the greatest rarity in Great Britain before 1933. Up till that date there were only about six records. In that year it suddenly appeared in south-west England, notably in Cornwall in considerable numbers. Since then it has become firmly established in that region and has been steadily extending its range eastwards and northwards. In Holland it made an equally remarkable and sudden appearance in the early 1930's and is now a regular resident in that country. In Denmark, however, it was first taken on the Island of Bornholm in the Baltic in 1950 and there again in 1952. The species is widespread in Europe, mainly in the western regions.

Minucia lunaris Schiff. Up till 1942 there were probably less than a dozen records of this large noctuid moths's occurrence in the British Isles. Most of the captures of this insect had been in the south of England. In the year mentioned the species was found to be well established and breeding in Kent and has since been found to be spreading through that county as well as into Sussex and Essex. The species which has always been indigenous in Holland, is fairly common in the West of Europe, but the only authenticated record from Denmark was in 1938.

Sedina buettneri Hering. This small noctuid was first discovered in the British Isles by the late Dr. K. G. Blair in a small marsh in the Isle of Wight in October 1945. So far this is the only locality for this species which is very local in Central and Western Europe. It was first met with in Holland in 1948 and a few examples have been obtained there each year since that date. In Denmark it was first recorded from Falster in 1945 and has now spread to Jutland. Its foodplant is chiefly *Carex acutiformis*.

Aplasta ononaria Fuessl. In the 1860's there was for a short time a small colony of this geometrid moth on the coast of Kent. The species was not observed again in England until 1932, also in Kent where a flourishing colony was discovered in 1938. Since then it has spread in that area. It is an insect of mainly western habitation in Europe, being quite common in in the north of France. It is unknown in Denmark and there is only one record for Holland, in 1938. Its larva feeds on *Ononis*.

(b) SPECIES WITH A MORE EASTERLY RANGE IN EUROPE

Hadena compta Fabr. The recent spread of this attractive noctuid in Europe is a very good example of the northerly trend of this species, for which there were not more than some half a dozen records in the British Isles up to 1948. In that year it was found to be breeding on a large scale in East Kent. Since then it has been extending its range rapidly up the east coast of England and has been reported from South Devon. It has had a parallel movement in Denmark where it was first observed in 1915 and has since spread steadily over the whole country. In Holland it has also extended its range in a similar way only during the past 20 years. Its larva feeds chiefly on species of *Dianthus*. It is fairly widespread in Central and Western Europe.

Calophasia lunula Hufn. Though this insect was reported early in the 19th century in England, it was not till 1939 that the first authentic record was made in Sussex. The next capture was not until 1951, from Kent. Since then it has become increasingly numerous, both in the larval state and as the imago, recently appearing in Essex. It was first noted in Denmark in 1938 and has now spread to the Skaw, the most northerly point of Jutland. In Holland where it was formerly rare, it has become quite common during the past 20 years. Its larval foodplant is *Linaria*. Its general range is over the whole of France and most of Central Europe.

Thalera fimbrialis Scop. Up till 1950 there had been only two records in the British Isles of this green geometer. In that year a number were taken in East Kent. It was found to be breeding regularly in that area where it is now well established as well as on the borders of Sussex. The species which is widespread in Western and Central Europe has always been a resident in both Holland and Denmark. It is evidently extending its range north-westwards by its apparently recent colonisation in England.

Euphyia luctuata Schiff. The first authentic example of this attractive geometer was recorded in 1924. It did not reappear till 1950 when it was found to be breeding in Sussex. In the following year it was obtained in Kent in some numbers among its foodplant *Epilobium angustifolium*. During the past five years it has spread rapidly in south-eastern England and is now abundant in many localities in that region. In Denmark it was first taken on Bornholm in 1944 and has since become quite common there, but as yet it has not been noted on the Danish mainland. In Holland, where it was formerly very local, it has been steadily extending its range in a similar manner as in England. It is widespread in Western Europe.

The following three species of the Tortricidae are of especial interest as falling within the category under review.

Eulia formosana Geyer. This little insect was first taken in England, in Surrey in 1945 among *Pinus silvestris*, its larval pabulum. During the last ten years it has become quite a regular resident in southern England where it had never been previously noted. It is a species with a southern trend in Europe, though it has been obtained near Paris.

Ptycholomoides aeriferana H.-S. This tortrix appeared for the first time in Kent in 1952 and has now been found in many parts of the Eastern Counties of England, chiefly among larch. In France it is described as an alpine species.

Adoxophyes orana von Rössler. This tortrix first made its appearance in Great Britain also in 1950, in Kent, among the apple orchards in which it caused considerable damage. It is still spreading steadily inland in the south-eastern regions of England. In Germany and in Central Europe it has also been showing a similar surge northwards, especially in Holland and Belgium where it was unknown until 1940. It has since been doing a great deal of damage in both these countries.

GROUP II

Species of rather sporadic occurrence which appear to be in the process of becoming resident in the British Isles or are equally newcomers to the more northerly regions of Europe.

Tathorhyncus exsiccata Lederer. This remarkable noctuid emanating from the subtropical regions of Europe and from the Middle East, was first secured in England in the spring of 1952. The first record for France was also made at this period. In the succeeding years a further five records have been made, all in the south of England, denoting a definite movement of this species in a northerly direction. It has as yet not been reported from either Holland or Denmark.

Lithophane lapidea Hübn. This is another noctuid of especial interest since its chief habitat is the Mediterranean regions and the Levant. It was first recorded for the British Isles in 1951 by the late Dr. Blair in the Isle of Wight. It reappeared there in 1955 and also in Sussex with a few specimens, but in October 1956 it was obtained quite commonly in both areas. Its chief pabulum is cypress which is prevalent all over the south of England. There is therefore every evidence that it is now a regular breeding species. So far it had not been recorded in Holland or Denmark.

Bryophila raptricula Hübn. This small noctuid was first obtained in the British Isles in Sussex, in 1954, while another was taken in Hampshire in 1955. In Denmark, it was first noted in 1904 on Bornholm where it has become quite plentiful, eventually appearing in Jutland in 1949. In Holland it was originally observed in 1941 and is now spreading rapidly in that country, especially in the southern region, thus pointing to a generally northward movement of this species in recent years.

Cosymbia puppillaria Hübn. This geomtrid moth was also discovered by the late Dr. Blair in the Isle of Wight in 1947. Since then have been no less than ten British records, six occurring in 1956, all along the south coast as far as the Scilly Islands. Denmark claims a specimen in 1934 and Holland a single example in 1871. This is an insect of definite Mediterranean habitat, its larval foodplant being myrtle. Its recent appearance in England is most unexpected.

Jaspidea deceptoria Scop. This little noctuid was first recorded in Britain in 1948 from East Kent. Only eight examples have been noted since then up till 1956, all from the south-eastern corner of England. Its breeding headquarters have so far not been located. In Holland it has always been rare, but there have been sporadic captures as in England. Apparently it has increased its range in Belgium in recent times. It is fairly widespread in Eastern France, while in Denmark it was first obtained in 1914, but since 1930 it has spread rapidly and is now found all over that country.

Plusia confusa Steph. It was first noted from Essex in 1952, as a British species. Since then two or three examples have been obtained each year, all in the south-eastern quarter of England. In Holland it originally made its appearance in 1934. In 1945 two more were recorded from that country, then it increased rapidly each year until 1955 when nearly thirty were recorded. It was first reported from Denmark in 1934 and has subsequently been spreading steadily over that country.

The account given of the above species of Lepidoptera provides a great deal of evidence to show that there has been in recent years a definite movement to extend their range towards the north by some insects whose range just reaches the English Channel or the North Sea and by others of a far more southern distribution and habitat.

There is no doubt that the advent and use of mercury-vapour light as a source of attraction has been of increased assistance in studying and assessing the movement and migration routes of many moths of nocturnal habits. We are in the process of witnessing this phenomenon of a northward movement which has very likely been of a cyclic nature through the ages and brought about by periodic amelioration of the climate in the northerly latitudes of Europe and other parts of the world.

REFERENCES

Barrett, C. G. 1893 to 1907. Lepidoptera of the British Islands. Vols. 1 to 13.
Beirne, Bryan. 1952. Origin and history of the British Fauna.
de Worms, C. G. M. 1951. New additions to British Maccrolepidoptera during the past half century. *Entomologist's Gazette* 2: 153.
Hoffmeyer, Skat. 1948. De Danske Spindere, Aarhus.
Hoffmeyer, Skat. 1949. De Danske Ugler, Aarhus.
Hoffmeyer, Skat. 1952. De Danske Maalere, Aarhus.
Manley, Gordon. 1944. *Quart. J. Royal Met. Soc.* London 70: 197.
Manley, Gordon. 1953. *Idem.* 79: 561.
South, Richard M. 1939. British Moths.

The Dispersal of Insects by Human Agencies Across the North Atlantic

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ABSTRACT[1]

A large part of the insect species common to Europe and North America must be regarded as introduced into either continent, or both, this element amounting to more than 45 per cent. Species introduced from Europe into North America are about ten times as numerous as those transported in the opposite direction. This is explained by the peculiar character of ballast traffic in olden times, sailing vessels going in ballast almost exclusively on their way west, to Newfoundland and the Maritime Provinces of Canada on one hand, to the Pacific Northwest on the other. The main area of departure for these animals, mostly belonging to the soil fauna, was southwestern England. A contributing reason why the contingent of introduced European insects is particularly large in the regions mentioned is of course that the climate of these parts of the continent is most similar to that of western Europe.

[1] Included in the book, "The faunal connections between Europe and North America", published by *John Wiley and Sons* in 1957.

The Composition of the Canadian Coccinellid Fauna

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ABSTRACT

The coccinellid fauna of Canada can best be explained by considering five faunal zones, Arctic, Tundra, Boreal, Transition, and Mountain. The fauna of each zone, although overlapping, is distinct, and originates somewhat differently in each case. Comparing the distribution of the various Coccinellidae with those of the neotropical and palaearctic regions gives an indication of the origins of the several faunal parts. Three groups of genera make up the native fauna, one from South America, one from southwestern United States, and one directly from the palaearctic region. These faunae represent three distinct waves of invasion from the Old World, separated from one another by climatic and geographic barriers. The first wave entered the New World area during a warm period in the north Pacific. A second wave entered during a subsequent cool period. And a final invasion of recent forms came in after the retreat of the glaciers. Genera resulting from the first invasion are poorly represented in Canada, being found only along the southern border. Representatives of the second invasion are more numerous, especially in the western mountain region. Genera arising from the third-final invasion form the bulk of the widespread Coccinellidae found in Canada, and are distributed throughout the whole of the boreal region.

Preliminary Observations on the Origin of Some Nearctic Bird Lice (Mallophaga)

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ABSTRACT

A study of the host-parasite distribution of the biting lice parasitizing the Nearctic gallinaceous birds indicates that the distribution patterns of the lice are related to the geographical area in which the host group evolved. The site of origin of the parasite group is still discernible despite the penetration of the host group into a new area. Some widespread aquatic birds as the skimmers present special problems and their site of origin is not apparent by this approach.

INTRODUCTION

The distribution of Mallophaga has been traditionally interpreted along strict host-parasite lines. In some instances geographic factors have played a role in producing present-day distributional patterns. Despite the lack of a fossil record, the distribution of Mallophaga genera may often be used as means of faunal analysis. Vanzolini and Guimarães (1955) have made an admirable study of the zoogeographic relations of South American mammals and their lice. Jellison (1942) has made a similar analysis for the Nearctic rodents. As yet, no comparable study has been made of the entire North American mammal fauna. The purpose of the present paper is to present some of the results of investigations by the author on avian Mallophaga which may serve to demonstrate the utility of these ectoparasites in a study of this nature. Vanzolini and Guimarães emphasize, "No phylogenetic or zoogeographical discussions should be based on isolated cases, but rather on patterns of infestation." This practice has been followed and it is hoped that future investigators will assume the same approach.

The zoogeographic scheme proposed by Schmidt (1954) will be used throughout this paper to designate the faunal realms and regions.

LICE OF GALLINACEOUS BIRDS

The order Galliformes (megapodes, curassows, pheasants and hoatzin) is world-wide in occurrence. Two suborders are recognized (Wetmore, 1951); a single abberant Neotropical species, the hoatzin, comprises the Opisthocomi and the remaining form the Galli. The Cracoidea contain two living groups, the Megapodidae of the Australian and Oceanian regions and the Oriental subregion, and the Cracidae of the Neotropical region and Central American province of the Caribbean subregion. Most of the well-known forms are members of the Phasianoidea. The Tetraonidae or grouse are typical of the Holarctic. The Phasianidae contain three subfamilies; the Phasianinae (pheasants and peacocks) and the Perdicinae (partridges) are endemic to the Old World while the Odontophorinae (quail) are only present in the New World. The Meleagridae (turkeys) are confined to the Nearctic and Caribbean transitional. The Numididae (guinea fowl) are present in the Ethiopian and Malagasy subregions.

Table I serves to summarize the distribution of Mallophaga genera on the Galli.[1] *Colpocephalum* is not included because of the paucity of authentic records. In examining this chart it may be observed that certain parasite genera as *Goniodes*, *Oxylipeurus* and *Menacanthus* have a fairly wide host distribution; others as *Cuclotogaster*, *Chelopistes* and *Clayia* have a more restricted host distribution. *Passonomedia*, *Labicotes*, *Pachyskelotes*, *Numidicola* and *Somaphantus* are each known from a single host. If the two dubious records are not considered, only a single genus, *Oxylipeurus*, of the eight found on the Cracoidea is common to both constituent families. A comparison among the families of the Phasianoidea shows that no single genus is common to all four families. Only *Goniodes* and *Menacanthus* occur on 3/4 of the families. If one compares genera which are common to two families it is seen that excluding the dubious record, 5/16 (31%) of the genera parasitizing the Phasianidae and Numididae are common to both families, 3/14 (21%) are shared between the Phasianidae and Tetraonidae, and Phasianidae and Meleagridae, 1/10 (10%) between Tetraonidae and Numididae, 1/9 (11%) between Numididae and Meleagridae and none are common among the Meleagridae and Tetraonidae. It is worth noting that the above relationships between families as indicated by the distribution of bird lice are quite close to those expressed by ornithologists.

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[1] The hoatzin is parasitized by *Hoazineus*, *Osculotes*, *Rallicola* (*Wilsoniella*) and *Laemobothrion* (*Eulaemobothrion*). The first three groups are only found on this host.

TABLE I. Distribution of Mallophaga Genera on the Galli.

	HOSTS							
	Cracoidea		Phasianoidea					
				Phasianidae				
MALLOPHAGA GENERA	Megapodidae	Cracidae	Tetraonidae	Phasianinae	Perdicinae	Odontophorinae	Meleagridae	Numididae
Ischnocera								
Lipeurus	X	0	0	X	X	0	0	X
Cuclotogaster	0	0	X[1]	X	X	0	0	0
Lagopoecus	0	0	X	X	X	X	0	0
Oxylipeurus	X	X	0	X	X	X	X	0
Goniocotes	0	0	X[2]	X	X	0	0	X
Goniodes	X	0	X	X	X	X	0	X
Chelopistes	0	X	0	X[3]	0	X	X	0
Passonomedia	0	0	0	0	0	M	0	0
Labicotes	0	M	0	0	0	0	0	0
Pachyskelotes	0	0	0	M	0	0	0	0
Amblycera								
Kelerimenopon	X	0	0	0	0	0	0	0
Cracimenopon	0	X	0	0	0	0	0	0
Desumenopon	0	0	0	0	0	X	0	0
Menopon	0	0	0	X	X	0	0	0
Clayia	0	0	0	X	0	0	0	X
Amyrsidea	X[4]	0	X	X	X	0	0	0
Menacanthus	0	X	0	X	X	X	X	X
Numidicola and *Somaphantus*	0	0	0	0	0	0	0	M

X = Widely distributed throughout host group.

O = Absent on host group.

M = Monotypic genus present on a single species in the host group.

X[1] *C. cameratus* (de Haan) on *Lyrurus tetrix* is the only known species on this family.

X[2] A dubious record, see footnote number 2.

X[3] *C. lervicola* (Clay) on *Lerwa lerwa* is the only known species on this subfamily.

X[4] *A. lativulvata* (Piaget) is the only known species of this genus on a member of the family. It has not been encountered since its description from a single female and is probably a dubious host record.

In the Galli, only the Phasianidae are divided into subfamilies. A comparison of the Phasianinae and Perdicinae shows a majority of the genera are common to both group (9/11 or 81%). Approximately 1/3 of the genera present on the Odontophorinae also occur on the Phasianinae and Perdicinae. An interesting feature of the quail subfamily is that its Mallophaga fauna is closely allied to that of the Meleagridae, a related family. The Cracidae, which are ornithologically remote from the Odontophorinae, share three of the nine genera on these two groups. This type of distribution can best be interpreted in terms of the sites of geographical origin of the host groups.

Lipeurus, *Cuclotogaster*, *Goniocotes*, *Kelerimenopon*, *Menopon* and *Clayia* are restricted to Galliform groups which evolved in the Old World. These six genera are all absent from birds of New World origin and in part are represented by ecological equivalents such as *Chelopistes*, *Cracimenopon* and *Desumenopon*. The wide distribution of *Lagopoecus* in the New World and its limited occurrence in the Old World points to a New World origin for the genus. Genera such as *Oxylipeurus*, *Goniodes*, *Amyrsidea* and *Menaconthus* are found on both New and Old World hosts and appear to be rather old forms.

A detailed consideration of the native Nearctic Galliformes and their lice will serve to substantiate these statements. There are four families, fourteen genera and twenty-one species of this order in this subregion (Hellmayr and Conover, 1942). Two species of Cracidae, both in the genus *Ortalis* (chacalacas), penetrate the lower limits of the Nearctic. Their fauna is characterized by *Chelopistes* and *Cracimenopon*. With the exception of these species, *Chelopistes meleagridis* (Linnaeus) and possibly *Chelopistes lervicola* (Clay), these two genera are exclusively Neotropical and Caribbean Transitional in distribution.

The seven genera of Tetraonidae in the Nearctic subregion (*Dendragopus*—grouse, *Lagopus*—ptarmigan, *Canachites*—spruce grouse, *Tympanachus*—prairie hen, *Bonasa*—ruffed grouse, *Pedioecetes*—sharp-tailed grouse and *Centrocercus*—sage grouse) are all parasitized by species of *Lagopoecus* and *Goniodes*. *Amyrsidea* probably exists on all genera, but has currently been recorded from only three. The three remaining Tetraonids, *Lyrurus*, *Tetrastes* and *Tetrao*, are restricted to the Palaearctic, while the previously mentioned *Lagopus* is circumpolar. The Palaearctic hosts are parasitized by the same Mallophaga genera as their Nearctic relatives. The conspicuous absence of *Lipeurus*, *Goniocotes* and *Cuclotogaster* (with two exceptions[2]) points to the Nearctic origin of the lice of this group.

All the Nearctic Phasianidae are in the subfamily Odontophorinae. This includes *Oreotyx* (plumed and mountain quail), *Callipepla* (scaled quail), *Lophortyx* (valley quail), *Colinus* (Bob white) and *Cyrtonyx* (Mearn's quail). *Lagopoecus* and *Goniodes* infest all the above genera. *Oxylipeurus* probably occurs on all members, but presently has been recorded only from *Callipepla*, *Colinus* and *Cyrtonyx*. Like the grouse, *Lipeurus*, *Goniocotes* and *Cuclotogaster* do not occur on the New World quail. *Chelopistes* replaces *Goniodes* on the genera of this family (*Odontophorus*, *Dendrortyx* and probably others) which are exclusively Caribbean Transitional and Neotropical in distribution. *Lagopoecus* is absent on these groups. The only deep Neotropical extensions of *Goniodes* and *Lagopoecus* are shown by the species present on *Colinus cristatus* which ranges between Salvador and Brazil. It is likely that *Chelopistes* evolved in North America during the Tertiary and after reunion with South America in the Pliocene pushed southward to Central and South America via genera such as *Odontophorus*. The absence of *Lagopoecus* cannot be attributed to competition as there is no other genus occupying its niche on the host.

Meleagris gallipavo, the turkey, is the sole Nearctic representative of the Meleagridae. Its fauna consists of only a *Chelopistes*, two species of *Oxylipeurus* and *Menacanthus stramineus* (Nitzsch). The first two genera point to a Nearctic origin for these lice. The *Menacanthus*, which is almost cosmopolitan in host and geographic distribution, is neutral insofar as indicating affinities

Due to the extensive taxonomic investigations of M. A. Carriker, Jr., Theresa Clay and K. C. Emerson we have a better knowledge of the Ischnocera of Nearctic Galliformes than those of virtually any other order in this region. Because of this background it is possible to postulate the possible zoogeographical history of these genera.

Goniodes and *Oxylipeurus* arrived fairly early in the Tertiary in the New World by means of the Bering land bridge. During the Miocene in North America the *Goniodes* stock evolved into *Chelopistes* and allied forms while *Oxylipeurus* diverged only at the species level. About the same time *Lagopoecus* evolved from the generalized *Degeeriella* stock in North America. Some species of *Lagopoecus* were able to enter the Old World via the Bering land bridge,[3] but were prevented from entering South America because of its isolation. *Oxylipeurus* never parasitized the Tetraonidae or became extinct on this group during this period. With the reunion of North and South America in the upper Pliocene, *Goniodes* and *Lagopoecus* were able to enter northern South America by means of the species on *Colinus cristatus*. They were unable to parasitize additional hosts because of the extensive speciation of *Chelopistes* and *Oxylipeurus* species groups on the Cracidae and their subsequent rapid speciation and radiation to the Odontophorinae and Meleagridae. *Chelopistes* on the whole has not been successful in the Nearctic subregion. It has only been able to reach the Nearctic-Caribbean Transition boundary in northern Mexico on the

[2] *Cuclotogaster cameratus* (de Haan) has been described from *Lyrurus tetrix*. This is probably a case of a successful host transference and subsequent speciation.

Goniocotes megalocephalus Uchida was described from a single female from a skin of *Tetrastes bonasia* from Sakhalin. No subsequent records of this species have been reported and there is the possibility that this specimen was a stray from some species of Phasianidae.

[3] Five species are known from the Phasianidae including three Palaearctic species (*L. colchicus* Emerson ex *Phasianus colchicus*, *L. meinertzhageni* Clay ex *Lerwa lerwa* and *L. ovatus* (Uchida) ex *Syrmaticus mikado*), one Oriental (*L. heterotypus* (Megnin) ex *Lophophorus impejanus*) and a single Ethiopian species (*L. waterstoni* (Bedford) ex *Francolinus gariepensis*).

Three are represented on the Tetraonidae; two are Palaearctic (*L. lyrurus* Clay ex *Lyrurus tetrix* and *L. pallidovittatus* (Grube) ex *Tetrao urogallus*) and one is Holarctic (*L. affinis* (Children) ex *Lagopus lagopus*).

Odontophorinae. Of the 35 described species, only a single one, *C. lervicola* (Clay) on *Lerwa lerwa* (Phasianinae), is known from the Palaearctic. The generic assignment of this species (Hopkins and Clay, 1952) deserves further consideration in view of its distribution.

The absence of *Goniocotes*, *Cuclotogaster* and *Lipeurus* from the New World could be interpreted in three ways. 1). These genera arose after the initial New World invasion of the primitive Galliform stock. 2). They did not reach the New World because of the filtering effect of the Bering land bridge which permitted *Goniodes* and *Oxylipeurus* access while excluding others. 3). These genera did enter but all became extinct because of the superiority of the forms which evolved in North America. The second interpretation appears to be the most probable one. *Lipeurus* and *Lagopoecus* both occur on several species of Old World pheasants and apparently coexist on the same host by inhabiting different feather tracts.

LICE OF THE SKIMMERS

Not all birds possess a fauna which is capable of analysis like the preceding order. Such a group is the Charadriiformes (gulls, terns, waders, skimmers, etc.) which contains many widespread shore and oceanic birds. One family will serve as an illustration. The Rhynchopidae (skimmers) has a single genus, *Rhynchops*, with three closely related species. *R. nigra* is present in the New World ranging between New Jersey and the Gulf coastal area in the United States southward to encompass most of the coastal and inland waters of South America. Other species are encountered in Africa and southern Asia. They are never found very far out at sea and the species on the different continents are completely isolated from one another. The Mallophaga fauna of the skimmers is remarkable because of its uniformity. *Quadraceps elongatus* (Piaget), 1885 and *Saemundssonia anisorhamphos* Timmermann, 1951 have been described from *R. flavirostris*, the African species. In 1952, specimens of *Quadriceps* were obtained from the American *R. nigra* and just this year K. C. Emerson provided *Saemundssonia* specimens from this host. A detailed comparison of this material with African specimens, including some of Timmermann's type series, showed no means of differentiating between populations of lice separated by several thousand miles of ocean. Despite a long temporal separation, there has been no visible speciation of these two species. In terms of our modern species concept, the Ethiopian and American populations of these Mallophaga deserve separate species names. This is the first known situation of this kind for this order of insects.

Mayr (1946) states that the present relationships among the skimmers indicates an extremely slow evolutionary rate or an enormous capacity for transoceanic dispersal. The habits of these birds would tend to negate the latter suggestion.

SUMMARY

It has been possible to adaquately treat only a small portion of the Nearctic bird lice —less than 10%. The choice of groups has been limited to those having a sound taxonomy and good distributional data. But it is believed that the general patterns present in the Galliformes should be perceived in other orders.

Unlike the dispersal patterns of many insect groups such as the termites (Emerson, 1955), saturniid moths and the mosquito genus *Culex* (Ross, 1953), which can be traced back to the Mesozoic, the Mallophaga have a later period of initial dispersal. This is based on the fact that modern bird orders did not appear until the early Tertiary (Romer, 1945). The availability of a new niche provided the basis for the rapid evolution of a new insect order, the Mallophaga, in a relatively short time.

The contemporary Nearctic Mallophaga fauna may be resolved into several faunal elements. The oldest consists of an Old World element, which entered via the Bering land bridge. Certain components of this have persisted today while others have evolved into new genera and species groups in North America during its separation from South America during the Tertiary. The largest portion of the Nearctic Mallophaga fauna appears to have evolved in America north of Mexico with a few members later joining the Central and South American fauna. None of the ancient Neotropical groups which evolved in South America during the long Tertiary isolation have made contributions to the Nearctic Mallophaga fauna. The filter bridge effect has been very apparent. After the initial dissemination through the Bering land bridge, little movement from the New World to the Old World has occurred. The lice of oceanic and aquatic birds of world-wide distribution present special problems and at present remain an unanalyzed component.

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REFERENCES

Emerson, A. E. 1955. Geographical origins and dispersions of termite genera. *Fieldiana: Zoology* 37: 465–521.

Hellmayr, C. E., and Boardman Conover. 1942. Catalogue of birds of the Americas. *Zool. Ser. Field Mus. Nat. Hist.* 13, part I, no. 1.

Hopkins, G. H. E., and Theresa Clay. 1952. A check list of the genera and species of Mallophaga. *Brit. Mus. (Nat. Hist.)*, London, England.

Jellison, W. L. 1942. Host distribution of lice on native American rodents north of Mexico. *Jour. Mammal.* 23: 245–250.

Mayr, Ernst. 1946. History of the North American bird fauna. *Wilson Bull.* 58: 1–41.

Romer, A. S. 1945. Vertebrate paleontology, 2nd ed., *University of Chicago Press*, Chicago, Ill.

Ross, H. H. 1953. On the origin and composition of the Nearctic insect fauna. *Evolution* 7: 145–158.

Schmidt, K. P. 1954. Faunal realms, regions and provinces. *Quart. Rev. Biol.* 29: 322–330.

Vanzolini, P. E., and L. R. Guimarães. 1955. Lice and the history of South American land mammals. *Rev. Bras. Ent.* 3: 13–45.

Wetmore, Alexander. 1951. A revised classification for the birds of the world. *Smithsonian Misc. Coll.* 117(4).

The Origin and Distribution of the Thrips of the Grande Prairie

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ABSTRACT[1]

The Grande Prairie is a treeless area of the midwestern part of the United States. It differs greatly from the Great Plains grassland, which is also called prairie, not only in biotic composition but also in edaphic, climatic, and topographic conditions. The Grande Prairie, exclusive of the hill balds, is a moist to wet grassland flourishing in a climate suitable to forests and its plants and animals are largely of southeastern origins. Its existence depends upon poor drainage, a feature brought about by the flattening actions of the prehistoric glaciers, upon the preemption of the glaciated areas by Andropogon *and other grasses and herbs before forests had an opportunity to reoccupy the same area, and upon the ability of the* Andropogon-Spartina-Scirpus *series of plants to hold their own against forest invaders. Relicts of the Grande Prairie to the east are indicative of past periods of immature drainage and of early invasions of moist loving grasses, rather than of a Xerothermic period or a Climatic optimum, many opinions in the literature to the contrary notwithstanding.*

The thrips of the Grande Prairie are relatively few in number of species and most are of southeastern origins. Truly western thrips are mostly confined to the west of the hundredth meridian, and none enters into the Grande Prairie. Several thrips introduced from Europe and several thrips of possible holarctic distribution have become established in the Grande Prairie presumably in recent times.

[1] The complete text will be published as "The thrips of Illinois" in the *Bulletin of the Illinois State Natural History Survey.*

Notes on the History and Distribution of the Carrot Rust Fly, *Psila rosae* (F.) (Diptera: Psilidae)[1]

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INTRODUCTION

The carrot rust fly has been known in Canada since 1885 when Fletcher (1886) reared specimens from infested carrots obtained on the Ottawa market. The pest is of European origin and has been found in many countries of Europe and more recently in New Zealand.

The carrot rust fly, as the name implies, attacks carrots and related crops such as celery, dill, parsley, and parsnips.

The writer was concerned with biology and control studies of this pest on susceptible crops grown on muck soil in the Bradford Marshes of Ontario, Canada. Frequently, this insect caused complete crop losses in celery and carrots.

HISTORY AND DISTRIBUTION

The carrot rust fly was described by Fabricius (1794). It was taken on rose foliage at Kiel in Germany. Extensive damage has been done by the pest in the following European countries: Germany, France, Italy, Switzerland, Czechoslovakia, European Russia, Crimea, Austria, Poland, Holland, Denmark, Sweden, Norway, Latvia, Finland, England, Ireland, Scotland and Wales.

The pest was discovered in North America in 1885 at Ottawa, Ontario, Canada. Fletcher (1886) stated, "During the present winter, I received from Professor Guignard of Ottawa some specimens of carrots purchased on the market, which were much mined by small white maggots. These have produced in the breeding jars, the carrot rust fly (*P. rosae*), so injurious in England". Later Fletcher (1887) reported the pest from Montreal and Quebec City, Quebec, and from Nepean, Ontario. By 1897 (Fletcher 1898) the pest was established in the Canadian Maritimes.

Harvey (1894) stated that storage carrots in Maine were found to be infested with carrot rust fly. This is the first record of the pest in the United States. In New York State, carrots and celery were extensively damaged near Broadalbin, according to Felt (1902).

In 1904 a severe outbreak occurred near Barrie, Ontario (Lochead 1905). This is only 20 miles from the Bradford Marshes where the writer conducted biology and control studies on the pest.

From 1910 to 1930, many reports from all of Eastern Canada and many of the Northern States are on record. For example: Chapais (1910) reported infestations east of Quebec City; Hewitt (1915), and Gibson (1915), damaged crops in Ontario, Quebec and the Maritimes; Du Porte (1916), infested carrots around Ste. Anne de Bellevue; Britton (1928) stated that the pest had done considerable damage to carrots in Connecticut in 1927.

Gorham (1934) gave a detailed account of the carrot rust fly and described its history and distribution up to that date. He stated that the insect was prevalent in all of eastern Canada, having been found as far west as Sault Ste. Marie in Ontario.

The following states of the United States of America were reported by Whitcomb (1938) to be inhabited by the carrot rust fly: Maine, New York, New Hampshire, Massachusetts, Michigan, Ohio, Rhode Island, and Connecticut. The pest was also recorded in Washington, New Jersey and Pennsylvania. Museum specimens were present in Idaho and Colorado. The Colorado specimens were taken near Laramie, Wyoming. There are, however, no records in the Wyoming files of the pest ever occurring in that state.

Since 1938 serious damage has been caused to susceptible crops, especially carrots and celery in the Pacific coast states of Washington (Hanson and Webster, 1941) and Oregon (Morrison. *et al.*, 1945).

The first occurrence of the pest in British Columbia was near Vancouver in 1936 but, according to Glendenning (1946), no control measures were undertaken until 1939.

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[1] Part of this paper was presented by the author to the faculty of the Graduate School at Cornell University, Ithaca, N.Y., in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

The insect now occurs on Vancouver Island and inland up the Fraser Valley, the Okanagan Valley, and as far east as Nelson.

Doane (1950) stated that the carrot rust fly had been taken in the Rib Lake area of Wisconsin.

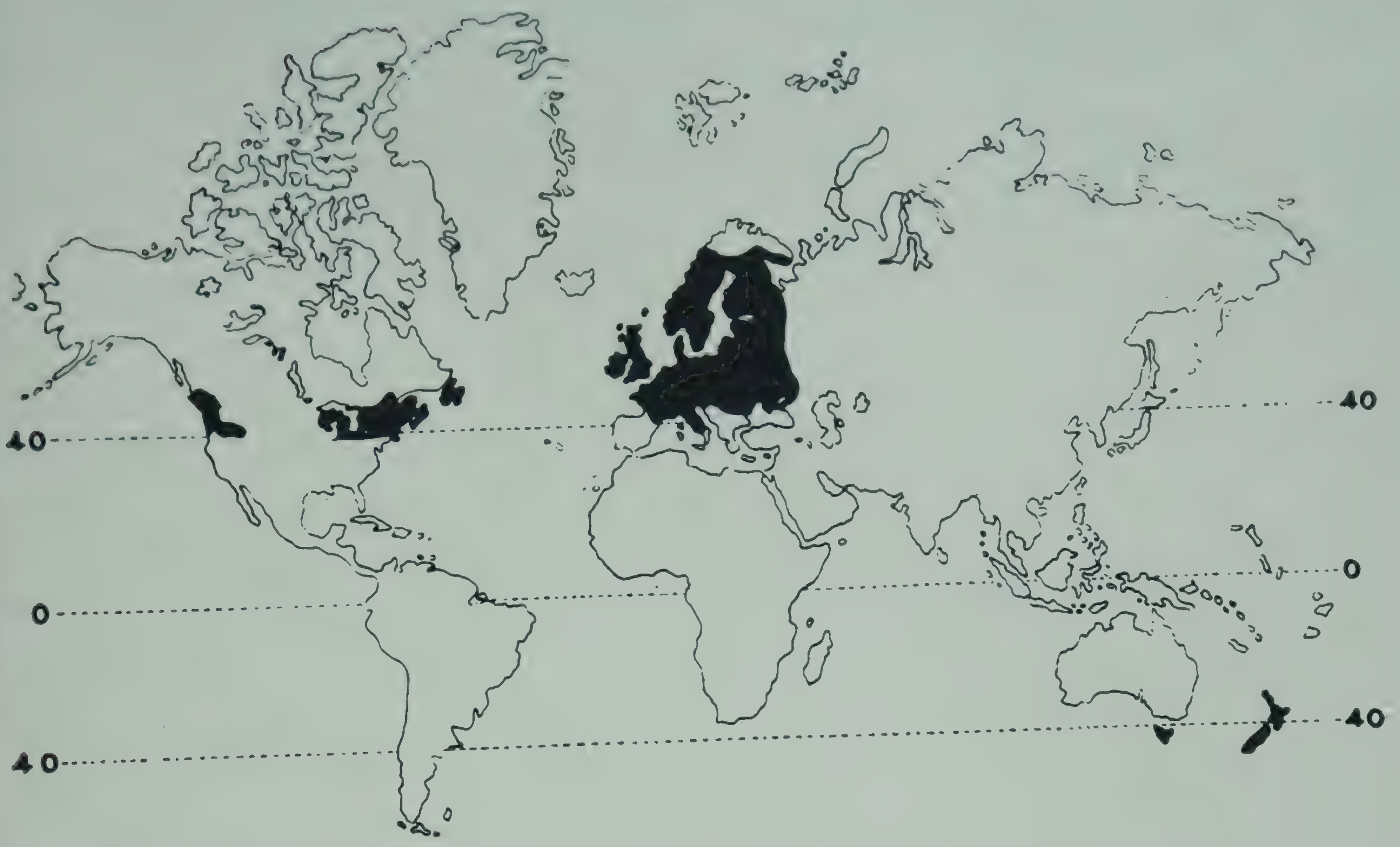
Wright (1951) found records of the pest from carrots at Urbana and Westmount, Illinois in 1942 and 1947, respectively.

Muggeridge (1933) reported the pest from New Zealand where it occurred near Auckland in 1931. Since then, the pest has spread to the South Island where it is doing severe damage.

Table I shows the earliest record discovered by the writer of the country, author and year of publication in which the pest was reported. Fig. 1 shows the world distribution and Fig. 2 the North American distribution of the carrot rust fly.

TABLE I.—History and Distribution of the Carrot Rust Fly.

Country	Author	Year of Publication
Austria	Wahl	1920
Canada:		
Ontario	Fletcher	1886
Quebec	Fletcher	1888
New Brunswick	Fletcher	1896
Nova Scotia	Brittain	1914
Prince Edward Island	Hewitt	1914
Newfoundland	Banks	1936
British Columbia	Glendenning	1938
Czechoslovakia	Fiala	1939
Denmark	Ferdinandsen	1919
Finland	Hukkinen	1925
France	Macquart	1835
Germany	Fabricius	1794
Great Britain:		
England	Curtis	1829
Ireland	Walker	1853
Scotland	Walker	1853
Wales	Thompson	1930
Holland	Ritzema Bos	1914
Italy	Berlese	1915
Latvia	Ozols	1927
New Zealand	Muggeridge	1933
Norway	Schoyen, W. M.	1894
Poland	Woroniecka	1923
Russia	Vassiliev	1913
Sweden	Fallen	1825
Switzerland	Faes	1935
United States:		
Maine	Harvey	1894
New York	Felt	1902
Michigan	Pettit	1914
Massachusetts	Fernald	1917
Oregon	Cole and Lovett	1921
Vermont	Johnson	1925
New Hampshire	Johnson	1925
Connecticut	Britton	1928
Pennsylvanua	MacLeod	1929
New Jersey	Headlee	1930
Ohio	Pierstorff and Parks	1932
Washington	Hanson and Webster	1937
Idaho	Whitcomb	1938
Rhode Island	Whitcomb	1938
Wisconsin	Doane	1950
Illinois	Wright	1951
Wyoming	List	1951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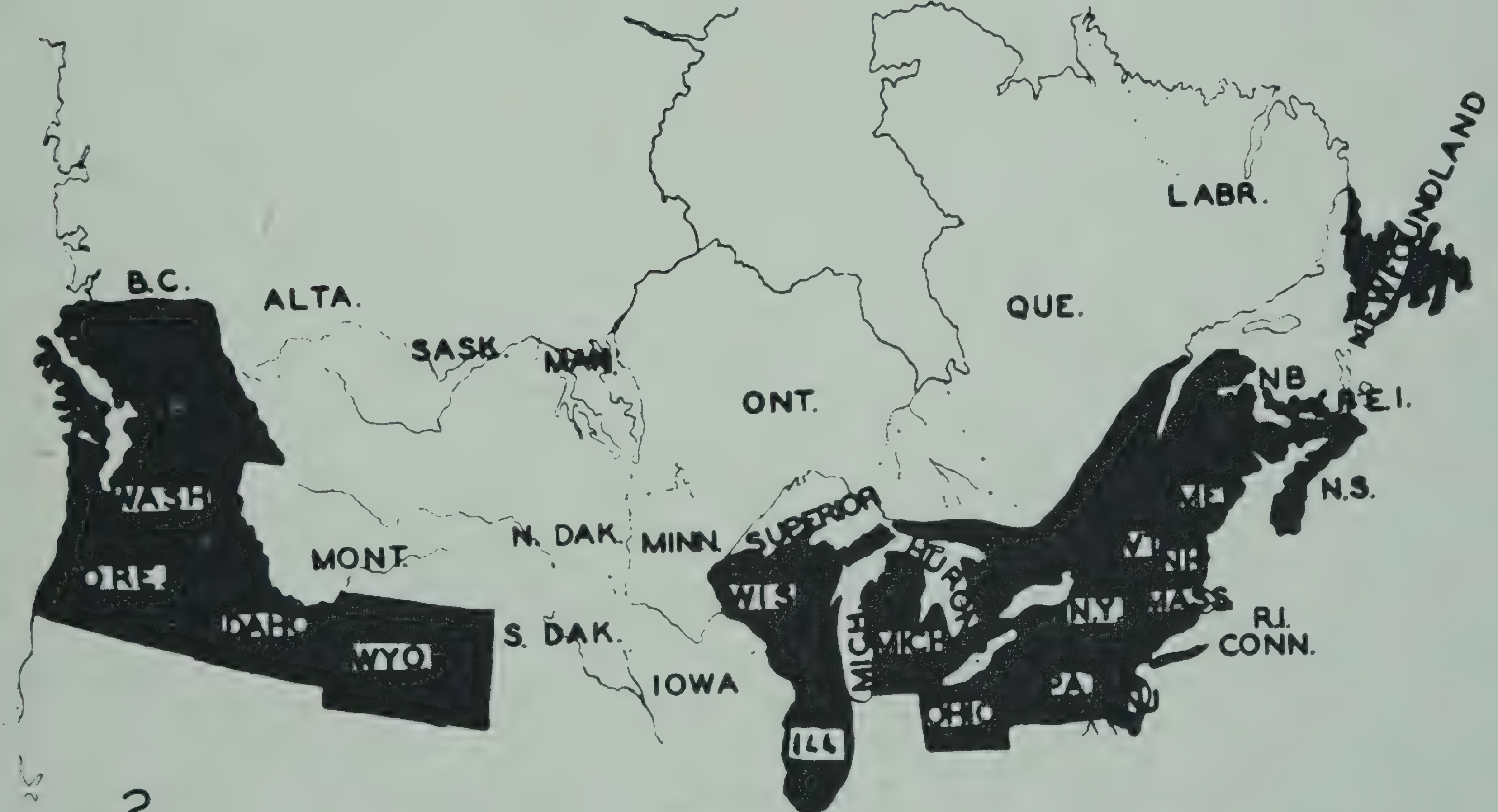
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WYO.
N. DAK.
S. DAK.
MINN.
IOWA
WIS.
SUPERIOR
HURON
MICH.
MICH.
ILL.
OHIO
PA.
N.Y.
VT.
N.H.
ME.
MASS.
R.I.
CONN.

2

Fig. 1. World distribution of the carrot rust fly. Fig. 2. North American distribution of the carrot rust fly.

DISCUSSION AND SUMMARY

This paper is essentially an attempt to show the geographical distribution of the carrot rust fly. A chronological thread may be evident. In 1907 Chittenden suggested that the carrot rust fly would be limited to the northern United States and Canada or south to about 40° north latitude. His prediction was based on European records. Essentially he was correct for with few exceptions the pest has remained within his predicted boundaries in the northern hemisphere. However, no one predicted the appearance of the pest in New Zealand. Here in the southern hemisphere the insect seems to be thriving on South Island more than on North Island. Therefore, it would seem from the geographical distribution of the pest that temperature is a limiting factor, although humidity and closeness to large bodies of water may also be very important.

REFERENCES

Banks, A. B. 1936. Common insect pests and their control. *Newfoundland, Dept. Nat. Resources, Agri. Ser., Bull.* 4: 22.

Berlese, A. 1915. *Psila rosae* Fab. pp. 167–168. *In* Entomologia Agraria. Florence.

Brittain, W. H. 1914. Pests of the year in Nova Scotia. *Canada Agr. Gaz.* 10: 795–797.

Britton, W. E. 1928. Twenty-seventh report of the State Entomologist of Connecticut. *Connecticut Agr. Exp. Sta. Bull.* 294: 198–299.

Chapais, J. C. 1910. The carrot fly. *Quebec Soc. Protection Plants Rept.* 2: 42–45.

Chittenden, F. H. 1907. The carrot rust fly. pp. 176–179. *In* Insects injurious to vegetables. *Orange Judd Co.,* New York, N.Y.

Cole, F. R., and A. L. Lovett. 1921. An annotated list of the Oregon Diptera. *Proc. California Academy of Sciences* 11: 332.

Curtis, J. 1829. The carrot fly. p. 231. *In* Guide to an arrangement of British insects being a guide catalogue of all the species hitherto discovered in Great Britain and Ireland. *Wesley and Davis,* London, England.

Doane, C. C. 1950. Personal correspondence.

Du Porte, E. M. 1916. Insect notes 1915. *Quebec Soc. Protection Plants Rept.* 8: 77.

Fabricius, J. C. 1794. *Musca rosae. Entomologia Systematica* 4: 356.

Faes, H. 1935. Rapport annuel station fédérale d'essai viticoles à Lausanne et Domaine de Pully. *Landwirtschaftliches Jahrbuch der Schweiz* 49: 619–664.

Fallen, C. F. 1825. Opomyzidae. *Diptera Sveciae* 2: 8–10. Lund, Sweden.

Felt, E. P. 1902. Insects in New York. *Country Gentleman* 67: 265, 290–291, 308.

Ferdinandsen, C., J. Lind, S. Rostrup and F. Kolpin-Ravn. 1919. Report of insect pests and diseases of the field and orchard in 1916–17. *Tidsskrift for Planteavl* 26: 317–318. (In Danish).

Fernald, H. T. 1917. Department of Entomology. *Massachusetts Agr. Exp. Sta. Rept.* 29: 78–79.

Fiala, F. 1939. Report on adverse factors affecting cultivated plants in Eastern Slovakia and in Carpathian Ruthenia in the Agricultural year 1937–38. *Ochrana Rostlin* 15: 23–26.

Fletcher, J. 1886. Carrot fly. *Canada Department of Agriculture, Entomologists Rept.* for 1885: 15.

Fletcher, J. 1888. Report of the entomologist and botanist. *Canada Exp. Farms Rept.* for 1887: 21.

Fletcher, J. 1896. Report of the entomologist and botanist. *Canada Exp. Farms Rept.* for 1895: 135.

Fletcher, J. 1898. Report of the entomologist and botanist. *Canada Exp. Farms Rept.* for 1897: 196–198.

Glendenning, R. 1938. Insects of the season on the lower mainland of British Columbia. *Canadian Insect Pest Rev.* 16: 71.

Gorham, R. P. 1934. Control of the carrot rust fly, *Psila rosae* Fab. *Quebec Soc. Protection of Plants Rept.* 25–26: 90–96. (French edition pp. 92–96).

Hanson, A. J., and R. L. Webster. 1941. The carrot rust fly. *Washington Agr. Exp. Sta. Bull.* 405: 1–24.

Harvey, F. L. 1894. Report of the botanist and entomologist. *Maine Agr. Exp. Sta. Rept.* for 1893: 178–180.

Headlee, T. J. 1930. Carrot rust fly. *New Jersey State Hort. Soc. Proc.* for 1926: 30.

Hewitt, G. C. 1914. Division of Entomology. *Canada Dept. of Agr. Rept.* for the year ending March 31, 1914: 851–876.

Hewitt, C. G. 1915. Division of Entomology. *Canada Dept. of Agr. Rept.* for the year ending March 31, 1915: 864.

Hukkinen, Y. 1925. Communication on the pests of cultivated plants in North Finland. *Maatalouskoelaitoksen Tietesllisia Julkaisuja* 2: 1–164. Abst. *In* Rev. Appl. Entom. Sec. A. 15: 315. 1927.

Johnson, C. W. 1925. *Psila rosae*. p. 269. *In* Fauna of New England: List of the Diptera. Boston Society of Natural History. Boston.

Korf and Boning. 1934. Celery flies and their control. *Prakt. Bl. Pflanzen.* 11: 261–265. Abst. *In* Rev. Appl. Entom. Sec. A. 22: 229. 1935.

List, G. M. 1951. Personal correspondence.

Lochead, W. 1905. Injurious insects of the season 1904. *Ontario Ent. Soc. Rept.* 35: 29.

MacLeod, G. F. 1929. Vegetable garden insects. *Pennsylvania Agr. Exp. Sta. Cir.* 122: 25.

Macquart, M. 1835. Psilidae. Histoire naturelle des insectes. Dipteres 2: 420–421. *Pourrot Freres,* Paris.

Meigen, J. W. 1826. *Psila rosae. Systematische Beschreibung der bekannten Europaischen Zweiflugeligin Insekten* 5: 355–361.

Morrison, H. E., D. C. Mote and W. B. Rasmussen. 1945. DDT to control the carrot rust fly. *Jour. Econ. Ent.* 38: 283.

Muggeridge, J. 1933. Some recently recorded exotic insect pests. *New Zealand Jour. Agr.* 47: 154–160.

Ozols, E., and J. Zirnits. 1927. Report of the Institute of Plant Protection. *Latvian Central Agr. Soc. Rept.* for the year 1926–1927: 14. (English summary).

Pettit, R. H. 1914. Report of the Entomologist. *Michigan Agr. Exp. Sta. Rept.* 53: 232.

Pierstorff, A. L., and T. H. Parks. 1932. Some seed and root infesting maggots. *Ohio Plant Diseases and Insect Notes* 3: 4.

Ritzema Bos. J. 1914. Diseases and damage caused by animals: Insects. Meded. R. Hoogere Land-Tuin en Boschbouwschool Wageningen. Abst. *In* Rev. Appl. Ent. Sec. A. 3: 200. 1915.

Schoyen, W. M. 1894. Beretning om Skadeinskter og plantesygdomme 1894. Abst. *In* Zeitschrift fur Pflanzenkrankheiten 6:31. 1896.

Thompson, H. W. 1930. Control of root flies in South Wales. *Welsh Jour. Agr.* 6: 295–301.

Vassiliev, E. M. 1913. On a method of fighting *Psila rosae* Fab. Abst. *In* Rev. Appl. Ent. Sec. A. 1: 463. 1913.

Wahl. B. 1920. The more important animal pests of our most common vegetables. Mitt. Landw.—bakter pflanzen. Abst. *In* Rev. Appl. Ent. Sec. A. 8: 261. 1920.

Walker, F. 1853. Psilides. Insecta Britannica 2: 297. *Lovell Reeve,* London, England.

Whitcomb, W. D. 1938. The carrot rust fly. *Massachusetts Agr. Exp. Sta. Bull.* 352: 1–36.

Woroniecka, J. 1923. Agricultural pests of Pulawy (Poland) and its environs in 1923. *Mem. Inst. Nat. Polon. Econ. Bur.* part 4: 341–359. Abst. *In* Rev. Appl. Ent. Sec. A. 13: 147. 1925.

Wright, J. M. 1951. Personal correspondence.

Peuplement odonatologique des Lacs tourbeux des hauts Plateaux de la Province de Québec

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RÉSUMÉ

Les multiples collections d'Odonates effectuées par l'auteur en trois secteurs de la province de Québec, région de l'Abitibi, du lac Mistassini et du parc du Mont Tremblant, permettent de mettre en relief les caractéristiques de la faune particulière à chaque habitat. Le but actuel est de montrer la complexité et la richesse de la faune des lacs tourbeux, ainsi que les différences qui existent entre les diverses régions.

Parmi les nombreuses espèces capturées aux lacs tourbeux et tourbières, l'auteur tâche de distinguer celles qui sont véritablement caractéristiques de ce type de lacs et qui sont habituellement présentes, soit dans tout le territoire couvert, soit dans l'une ou l'autre des régions, celles qui n'apparaissent dans ce milieu qu'occasionnellement et qui s'y reproduisent plus rarement, enfin celles dont la présence n'est qu'accidentelle; ces dernières proviennent d'habitats voisins et y retournent sans doute pour s'y reproduire.

Les lacs tourbeux, dont la faune odonatologique est comparée dans cette étude, sont situés dans trois secteurs de la province de Québec: Laurentides, Abitibi et Nouveau-Québec. Le secteur laurentien exploré fait partie du parc du Mont Tremblant et est arrosé par la Diable et la Boulé, deux affluents de la rivière Rouge qui se jette dans l'Outaouais. Dans ce territoire, les lacs sont nombreux et d'aspects variés. Nous nous occuperons ici des trois lacs suivants: aux Atocas, de la Grosse et Patricia qui, tous trois, possèdent des rives flottantes où dominent des sphaignes et des Ericacées. Leurs eaux sont brunes et acides.

Le lac aux Atocas n'est séparé de la Diable que par une zone de gravier d'environ 200 mètres de largeur. Ce rapprochement des eaux courantes favorise évidemment une faune odonatologique mixte. Le lac de la Grosse, éloigné d'environ un kilomètre de chacune des deux rivières ci-haut mentionnées, reçoit moins d'éléments faunistiques étrangers que le lac aux Atocas. A son voisinage toutefois se trouve le lac Bernard, lac à facies quasi identique, avec lequel les échanges peuvent être fréquents. Le lac "Patricia" que nous avons nommé ainsi parce que nous y avons repéré le *Leucorrhinia patricia*, est creusé au centre d'une plaine alluvionnaire sur la rive gauche de la Boulé. Il n'est séparé du lac Orignal, type de lac eutrophe, et de la rivière que par moins de 500 mètres. Ici encore, les possibilités d'échanges faunistiques entre micro-habitats voisins sont considérables.

Dans le secteur laurentien, la forme des tourbières et celle des lacs tourbeux fournissent de nombreux éléments communs et intéressants. La tourbière des Aulnes où prennent naissance deux ruisseaux coulant en des directions opposées, nord et sud, est située au pied d'un escarpement rocheux de grande élévation, à environ deux kilomètres de toute étendue lacustre. De petites mares permanentes suffisent à donner asile à une belle variété de larves d'Odonates dont les adultes errent au-dessus de la tourbière. La tourbière du lac Savane, formée sur une accumulation de cinq à six mètres de matières organiques, présente encore des zones suffisamment humides pour satisfaire aux exigences du développement de certains Odonates.

Le secteur abitibien, placé à la hauteur des terres qui portent leurs eaux vers la Baie James en direction sud-nord, compte sans doute plusieurs lacs tourbeux. Le lac Beaudoin, visité en 1942 et 1943 (Robert, 1944), n'a aucun émissaire et ses rives flottantes lui donnent exactement le facies des lacs mentionnés précédemment pour le parc du Mont Tremblant. Au moins un kilomètre le sépare des autres milieux aquatiques.

Le secteur du Nouveau-Québec, visité durant deux périodes de vingt jours en 1953, avoisine le lac Mistassini, cette mer intérieure qui déverse ses eaux dans la Baie James par la rivière Rupert. Dans ce territoire remarquablement plat, les lacs et tourbières deviennent contigus; il n'est guère possible d'isoler la faune odonatologique des uns et des autres. Nous avons surtout exploré de petits lacs tourbeux à un kilomètre au nord-est du Poste de

Mistassini, 50° 24′ N., d'autres lacs localisés sur l'île Marie-Victorin, 50° 43′ N. et les premiers lacs traversés en portageant du lac Mistassini au lac Albanel, vers le 50° 50′ N.

FAUNE DES LACS TOURBEUX

La faune odonatologique des lacs tourbeux est très variée, même en ne tenant aucun compte des nombreuses espèces des habitats voisins qui peuvent y faire des incursions momentanées et s'y reproduire à l'occasion. En effet, de vingt à trente espèces fréquentent de façon habituelle chacun des lacs des secteurs étudiés et peut-être notre inventaire est-il incomplet. En incorporant les espèces accidentellement capturées à ces lacs, nous dépassons la cinquantaine pour les lacs tourbeux des Laurentides (Tableau I).

TABLEAU I. Durée et étendue des observations.

	Parc du Mont Tremblant			Abitibi	Lac Mistassini		
	Lac de la Grosse	Lac aux Atocas	Lac Patricia	Lac Beaudoin	Autour du Poste	Ile M.-Victorin	Portage Albanel
Nombre total d'espèces récoltées:	40	35	26	20	20	17	20
Durée des observations:	3 ans	3 ans	2 ans	2 ans	1 an	1 an	1 an
Nombre de collections:	15	19	7	4	3	5	3

Les observations effectuées dans ces trois secteurs du Québec permettent de reconnaître dans cette faune des lacs tourbeux cinq séries d'éléments: 1o des espèces caractéristiques, généralement absentes de la plupart des autres milieux, du moins jamais aussi abondantes que dans le milieu étudié ici; ces espèces sont également susceptibles de se rencontrer dans tous les lacs de facies identique, quelle que soit leur latitude; 2o des espèces caractéristiques particulières à une région ou à certaines régions seulement; elles sont, en général, très abondantes dans le secteur où elles se trouvent, mais manquent complètement sous d'autres latitudes; 3o des espèces secondaires dont la présence paraît due à leur possibilité de se reproduire dans cet habitat, au moins à l'une ou l'autre des latitudes, mais non de façon exclusive; on les voit aussi dans d'autres habitats; 4o des espèces ubiquistes, habituelles dans ce milieu généralement acide, mais colonisant aussi d'autres milieux, lacs eutrophes ou oligotrophes; 5o des espèces accidentelles qui ne se reproduisent pas dans ce type de lac, mais proviennent d'habitats voisins et y retournent sans doute quand le temps de leur reproduction est venu; on pourrait donc les considérer comme étrangères à ce milieu.

D'une façon générale, les espèces ubiquistes et les espèces caractéristiques sont abondantes à tous les lacs tourbeux étudiés et il faudrait s'attendre à les retrouver avec ce même caractère d'abondance à tous les habitats similaires dans le territoire considéré. Parfois il arrive que l'une ou l'autre soit absente sans qu'on puisse préciser la raison exacte de cette disparition. Dans le secteur du parc du Mont Tremblant, l'*Enallagma cyathigerum* et le *Coenagrion interrogatum* manquent au lac aux Atocas; ils pullulent par ailleurs au lac de la Grosse et au lac Patricia. Le cas du *Leucorrhinia patricia* est le même; il a été repéré à un seul des trois lacs mentionnés dans cette étude et à l'une des tourbières; dans la région du lac Mistassini, ce minuscule *Leucorrhinia* caractérise plutôt les tourbières que les lacs tourbeux.

D'autre part, les espèces secondaires, et à plus forte raison les espèces accidentelles, sont beaucoup moins régulières dans l'association. Il peut même arriver que toutes fassent défaut; c'est ce que nous avons constaté en Abitibi et dans la région du lac Mistassini.

L'examen du tableau I permet de constater que la faune des lacs tourbeux laurentiens comporte un plus grand nombre d'espèces que les lacs tourbeux situés plus au nord, v.g. en Abitibi et au lac Mistassini. Ces derniers montrent toutefois des espèces absentes plus au sud, ou localisées dans d'autres habitats (Tableau II).

TABLEAU II. La faune odonatologique des lacs tourbeux.

1° Espèces caractéristiques à distribution générale:
Enallagma cyathigerum (Charp.)
Coenagrion interrogatum (Sélys)
Coenagrion resolutum (Hagen)
Nehalennia irene (Hagen)
Aeshna subarctica Walk.
Cordulia shurtleffi Scudd.
Somatochlora cingulata (Sélys)
Leucorrhinia hudsonica (Sélys)
Leucorrhinia glacialis Hagen
Leucorrhinia proxima Calvert

2° Espèces caractéristiques à distribution restreinte:
Parc du Mont Tremblant
Nehalennia gracilis Morse
Lestes eurinus Say
Aeshna tuberculifera Walk.
Dorocordulia libera (Sélys)
Nannothemis bella Uhler
Lac Mistassini:
Somatochlora albicincta (Burm.)
Somatochlora brevicincta Robert
Abitibi et lac Mistassini:
Aeshna sitchensis Hagen
Sympetrum danae (Sulzer)
Parc du Mont Tremblant et lac Mistassini:
Leucorrhinia patricia Walk.

3° Espèces secondaires:
Parc du Mont Tremblant:
Somatochlora williamsoni Walk.
Somatochlora elongata Scudd.
Libellula exusta julia Uhler
Sympetrum costiferum (Hagen)
Parc du Mont Tremblant et Abitibi:
Lestes congener Hagen

4° Espèces ubiquistes:
Enallagma boreale (Sélys)
Enallagma hageni (Walsh)
Lestes disjunctus Sélys
Aeshna eremita Scudd.
Aeshna interrupta Walk.
Aeshna umbrosa Walk.
Aeshna canadensis Walk.
Libellula quadrimaculata L.
Sympetrum obtrusum (Hagen)

5° Espèces accidentelles:
Parc du Mont Tremblant:
Agrion maculatum (Beauv.)
Agrion aequabile (Say)
Enallagma ebrium (Hagen)
Chromagrion conditum (Hagen)
Ischnura verticalis (Say)
Ophiogomphus mainensis Harvey
Ophiogomphus rupinsulensis (Walsh)
Gomphus brevis Hagen
Gomphus exilis Sélys
Gomphus spicatus Hagen
Gomphus borealis Needh.
Boyeria vinosa (Say)
Tetragoneuria canis MacL.
Helocordulia uhleri (Sélys)
Didymops transversa (Say)
Libellula lydia (Drury)
Sympetrum internum Mont.
Sympetrum vicinum (Hagen)
Leucorrhinia frigida Hagen
Leucorrhinia intacta (Hagen).

FAUNE DES TOURBIÈRES

Comme nous l'avons montré précédemment, la tourbière des Aulnes et celle du lac Savane possèdent des facies fort différentes: la première est isolée entre des crêtes montagneuses et parsemée de petites mares permanentes; un ruisselet y coule à découvert sur une certaine distance; la seconde ne possède ni étang, ni ruisseau d'écoulement; le tapis de sphaignes est toutefois flottant sur une masse d'eau souterraine d'environ deux mètres d'épaisseur.

La faune odonatologique décelée à ces deux tourbières possède peu d'éléments communs. Qu'il suffise de signaler: *Lestes dryas*, *L. disjunctus*, *Aeshna sitchensis*, *Cordulia shurtleffi*, *Sympetrum obtrusum*, *Leucorrhinia hudsonica*. Toutefois, les diverses espèces capturées dans ces tourbières ont été pour la plupart repérées également aux lacs tourbeux de la région et appartiennent surtout aux espèces caractéristiques de cet habitat ou à des espèces ubiquistes. A ces groupes, il faut rapporter vingt et une espèces à la tourbière des Aulnes et douze à la tourbière du lac Savane. Dans chaque cas, nous n'incluons pas une demi douzaine d'autres entités que nous considérons étrangères ou accidentelles à l'habitat, mais qui y ont été capturées une ou deux fois.

L'*Aeshna sitchensis*, abondamment représenté à la tourbière du lac Savane, trouve dans les sphaignes à demi submergées l'endroit idéal pour sa ponte. L'*Aeshna subarctica* y est moins nombreux mais affectionne le même habitat. Le *Leucorrhinia patricia*, relativement abondant à la tourbière des Aulnes, recherche davantage les mares découvertes qui parsèment les sols tourbeux là où l'apport d'eau souterraine est continu.

La trouvaille d'un frêle *Amphiagrion saucium* à la tourbière des Aulnes milite en faveur du renouvellement de l'eau des mares par un apport souterrain. Ce zygoptère est en effet caractéristique des sols sourceux. Il était d'autant plus surprenant de trouver l'espèce à cet endroit extrêmement isolé que, dans tout le reste du territoire, nous n'avons capturé qu'un seul autre spécimen.

CONCLUSION

Les lacs tourbeux favorisent le développement d'une faunule odonatologique extrêmement variée au sein de laquelle dominent des espèces vraiment caractéristiques de cet habitat. Le secteur des Laurentides, moins boréal que les secteurs abitibien et du Nouveau-Québec, héberge dans les lacs tourbeux plusieurs espèces méridionales, en particulier *Nehalennia gracilis*, *Lestes eurinus*, *Aeshna tuberculifera*, *Dorocordulia libera* et *Nannothemis bella*. Au contraire, les secteurs du Nouveau-Québec abritent plus régulièrement les espèces suivantes: *Somatochlora albicincta*, *S. brevicincta*, *Leucorrhinia patricia*, *Aeshna sitchensis* et *Sympetrum danae*.

Dans la région des Laurentides, les lacs et rivières sont nombreux et présentent une variété quasi infinie d'aspect annonçant des conditions écologiques également variées. D'autre part, la quasi contiguité de ces étendues d'eau permet facilement des échanges faunistiques entre les divers habitats. Les trois lacs tourbeux étudiés dans le parc du Mont Tremblant sont visités par beaucoup d'espèces étrangères que nous avons groupées comme accidentelles aux lacs tourbeux.

Les tourbières représentent le stade final d'évolution des lacs tourbeux; les Odonates qu'on y rencontre sont, en général, les mêmes qu'aux lacs tourbeux. Toutefois, leur pullulement est très faible; elles s'y rencontrent plutôt à l'état erratique. Seules quelques espèces semblent prospérer mieux que dans les lacs tourbeux; ainsi en est-il de l'*Aeshna sitchensis* et de *Leucorrhinia patricia*. Le *Lestes dryas* est parfois dans le même cas. La récolte de l'*Amphiagrion saucium* dans un habitat aussi solitaire que la tourbière des Aulnes était tout à fait inattendue.

Antérieurement à ces travaux, le *Nehalennia gracilis*, le *Leucorrhinia patricia* et le *Somatochlora brevicincta* n'avaient pas été récoltés dans la province de Québec. Le *Nehalennia gracilis* fut trouvé au lac aux Atocas en 1952 (Robert, 1953) et repris régulièrement depuis; c'est une des espèces les plus abondantes à chacun des lacs tourbeux étudiés dans le secteur laurentien. Le *L. patricia* était connu de l'Ontario septentrional et des Territoires du Nord-Ouest (Walker, 1940, 1942, 1943, 1951). Nous l'avons d'abord trouvé au lac Mistassini en 1953 et, en 1954 et 1955, nous avons récolté quelques individus à la tourbière des Aulnes et au lac Patricia. Le *S. brevicincta* est apparenté au *Somatochlora albicincta;* c'est une espèce que nous avons décrite en 1954 (Robert, 1954) et que nous avons capturée à deux lacs tourbeux de la région du lac Mistassini et au lac Georges, à La Ferme, Abitibi, le 29 août 1942.

BIBLIOGRAPHIE

Robert, Adrien. 1944. Premier aperçu sur les Odonates du comté d'Abitibi. *Nat. Canad.* 71: 149–171.

Robert, Adrien. 1953. Les Odonates du parc du Mont Tremblant. *Canad. Ent.* 85: 316–339.

Robert, Adrien. 1954. Un nouveau *Somatochlora* subarctique (Odonates, Corduliidae). *Canad. Ent.* 86: 419–422.

Walker, E. M. 1940. Odonata from the Patricia Portion of the Kenora district of Ontario with description of a new species of *Leucorrhinia*. *Canad. Ent.* 72: 4–15.

Walker, E. M. 1942. The female of *Leucorrhinia patricia* Walker, with further notes on the male. *Canad. Ent.* 74: 74–75.

Walker, E. M. 1943. The subarctic Odonata of North America. *Canad. Ent.* 75: 79–90.

Walker, E. M. 1951. The Odonata of the Northern Insect Survey. *Canad. Ent.* 83: 269–278.

A Method for the Analysis of Local Faunal Lists

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In attempting to give meaning to local lists of species of Diptera, it soon became obvious that the current zonal classifications according to Faunal Zones, Provinces, Biomes, etc.,[1] were unusable because hardly any of the species involved were distributed according to such zones. A second stumbling block was found in the lack of hierarchical arrangement of the zones to include species which might extend through two or more of the zones. A third impasse resulted from the fact that the zones are ecological, that is, based not only upon distribution of plants or animals, but also, or even primarily, upon climatic and soil factors. Fourthly, the schemes usually stop at the southern border of the United States.

The true nature of distributional patterns, furthermore, is probably not so much areal as one of centers or fasciae about which individuals are distributed in increasingly lesser abundance and proximity.

A basis for the analysis of local lists was therefore sought which might ultimately provide data usable in studies of more general significance. It seemed necessary to proceed first of all from actual distributional records of the animals involved.

The special cases deal with the Diptera of the family Ephydridae of the States of Florida and Michigan. Distributional data on Diptera is generally still scanty and vague. Due to recent work by Cresson and Sturtevant and Wheeler, the Ephydridae, although still far from being in a really good state for our purpose, are as good as any family in the order. Data on the Ephydridae of Florida was augmented by collections I made in the Woodruff Dam area where the States of Florida, Georgia, and Alabama come together. Especially abundant data on distribution in Michigan is available from collections made by Sabrosky, Dreisbach, myself, and others, for the List of the Diptera of Michigan now in process of compilation.

The first step consisted in mapping the known distribution of the species. Study of figures 1—12 of the distribution of selected species will show how little the current zonal classifications apply.

The second step consisted in the arrangement of the various distributions into categories or types and the alignment of those categories into further major categories. Preliminary and non-committal names were selected for a number of types of distribution. In the major arrangement the familiar scheme of Faunal Realms of Wallace and Sclater seems to apply, here touching the Nearctic and Neotropical, together with the later combination of elements of the Palaearctic and Nearctic into the Holarctic. The following categories have been distinguished:

1. Holartic

2. Nearctic
    a. Neoboreal — transcontinental in the north.
    b. Western — probably further divisible, but here including species which extend only slightly into the eastern half of the continent.
    c. Northeastern — centering apparently in the northeastern part of North America.
    d. Austroboreal — transcontinental, but not extending far northward; similar to the Lower Austral of Merriam.
    e. Austroriparian — the southeastern center, but with extensions beyond the commonly accepted boundaries of the zone usually so designated.

3. Neotropical
    a. Boreotropical — including tropical South America and a large part of North America.

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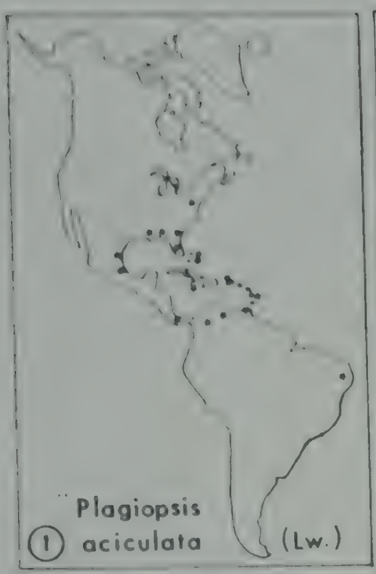
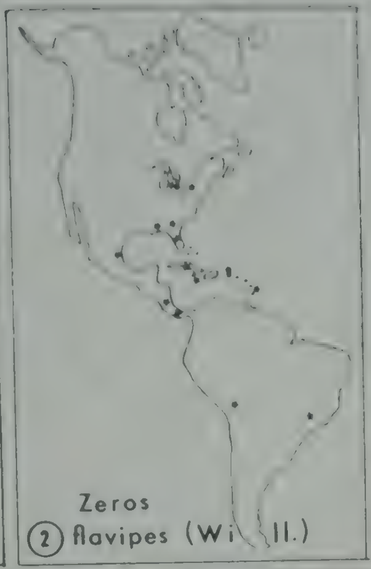
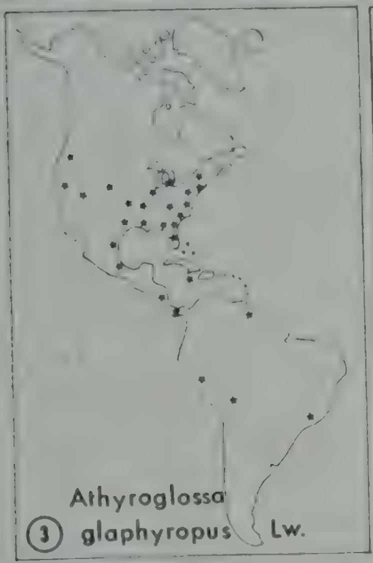
[1] "Current classifications" are such as those discussed in the following: Daubenmire, R. F. (1938). Merriam's life zones of North America. *Quart. Rev. Biol.* 13 (3); De Beaufort, L. F. (1951). Zoogeography of the Land and Fresh Waters. Sidgwick and Jackson, Ltd., London: Dice. L. R. (1943). The Biotic Provinces of North America. Univ. of Michigan Press, Ann Arbor; Muesebeck, C. F. W., and K. V. Krombein (1952). Life Zone Map. *Syst. Zool.* 1 (1): 24–25; Odum, E. P. (1953). Fundamentals of Ecology. W. B. Saunders Co., Philadelphia and London (esp. pp. 286–298); Van Dyke, E. C. (1939). The origin and distribution of the coleopterous insect fauna of North America. *Proc. 6th Pacific Sci. Cong.* **4**: 255–268.



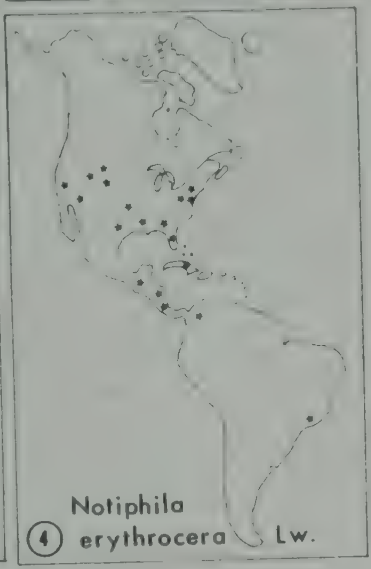
① Plagiopsis aciculata (Lw.)



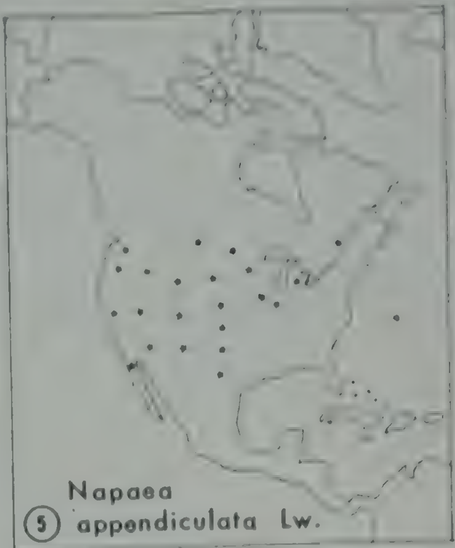
② Zeros flavipes (Will.)



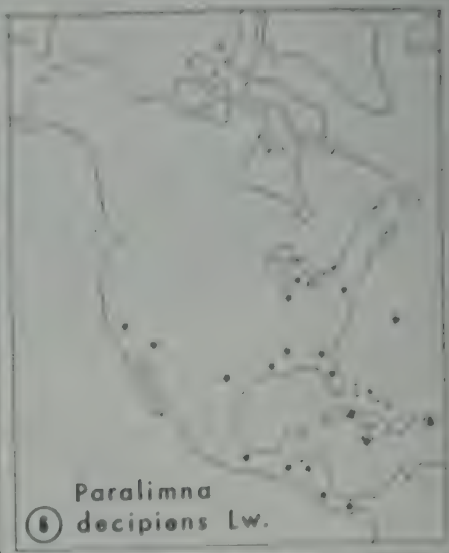
③ Athyroglossa glaphyropus Lw.



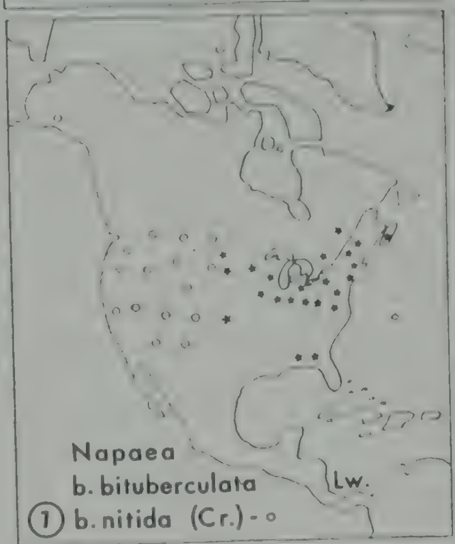
④ Notiphila erythrocera Lw.



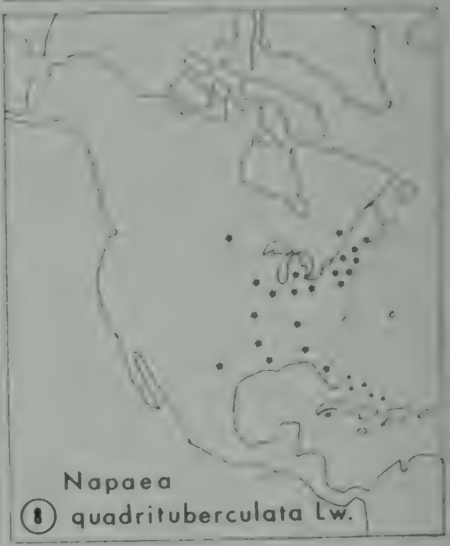
⑤ Napaea appendiculata Lw.



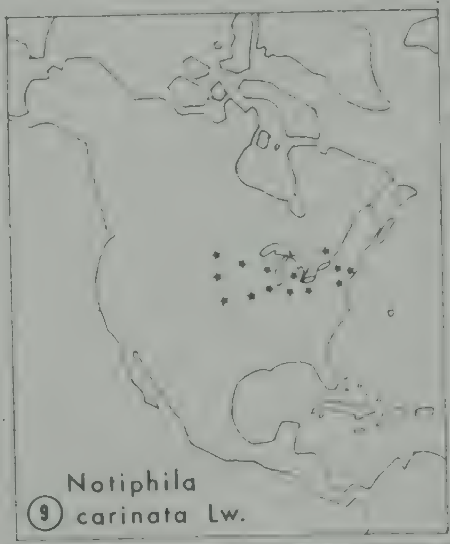
⑥ Paralimna decipiens Lw.



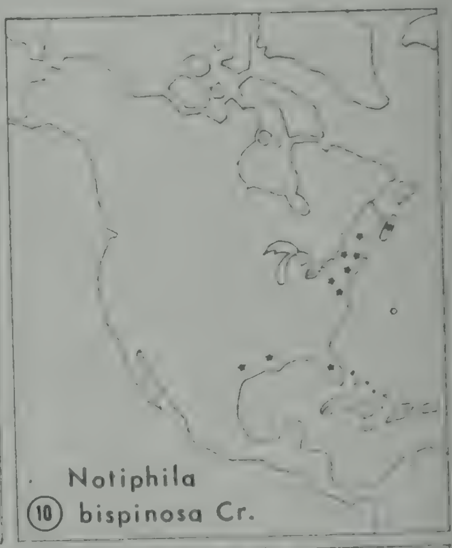
Napaea b. bituberculata Lw.
⑦ b. nitida (Cr.) - ○



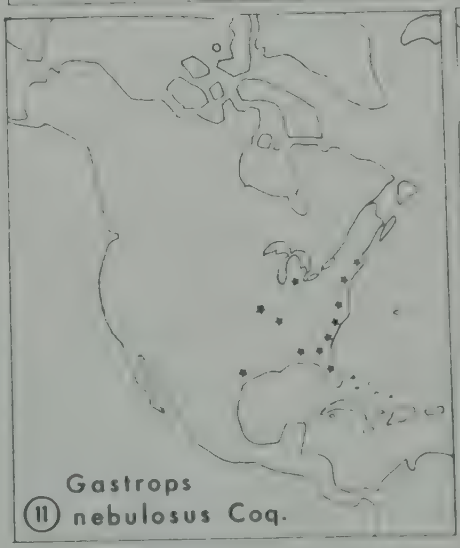
⑧ Napaea quadrituberculata Lw.



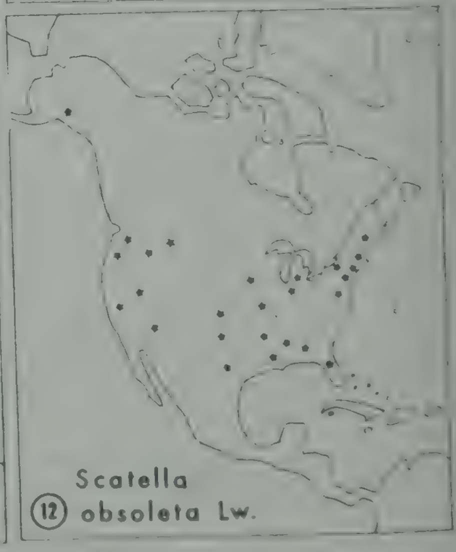
⑨ Notiphila carinata Lw.



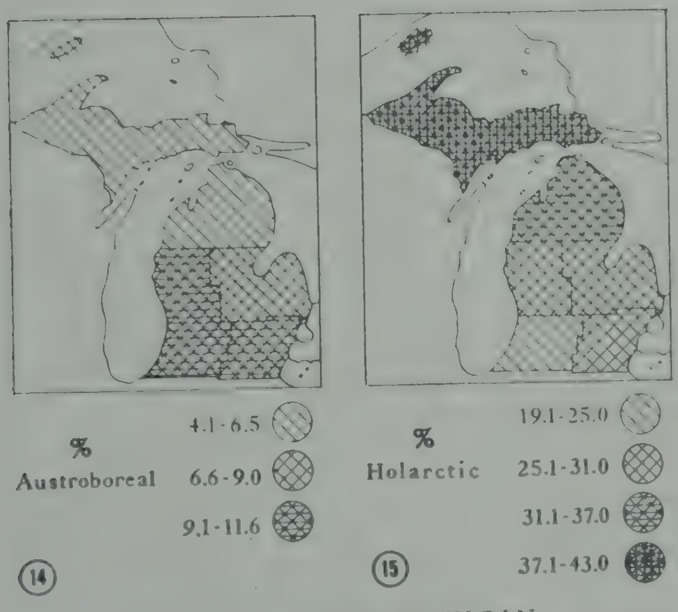
⑩ Notiphila bispinosa Cr.



⑪ Gastrops nebulosus Coq.



⑫ Scatella obsoleta Lw.



EPHYDRIDAE OF MICHIGAN

b. Caribbeotropical — in the Caribbean area, but also with extension well into South America.
c. Circumcaribbean — apparently centering in the islands of the Caribbean Sea, of the Gulf of Mexico, and the surrounding coastal areas.

4. Endemic to Florida — several forms known only from Florida may be considered either Austroriparian or Circumcaribbean, depending upon the area of Florida which they occupy and their relationships. (A few species are known only from Michigan, but it is unlikely that actual endemicity is involved here, but rather insufficient knowledge).

The third step was to calculate the percentages of the species falling into the several categories. The results may be tabulated as below and in the chart in Fig. 13.

MICHIGAN:	Holarctic	26 spp.	26.4%	
	Nearctic	73	68.9%	
	Western	6		5.7%
	Neoboreal	23		21.7%
	Northeastern	33		31.1%
	Austroboreal	7		6.6%
	Austroriparian	4		3.8%
	Neotropical	4	3.8%	
	(Boreotropical)			
	Reference doubtful	1	0.9%	
	Totals	106 spp.	100.0%	
FLORIDA:	Holarctic	9 spp.	13.4%	
	Nearctic	30	44.8%	
	Neoboreal	4		6.0%
	Northeastern	4		6.0%
	Austroboreal	12		18.0%
	Austroriparian	10		14.8%
	Neotropical	22 spp.	32.8%	
	Boreotropical	8		11.9%
	Caribbeotropical	8		11.9%
	Circumcaribbean	6		9.0%
	Endemic	5	7.5%	
	Reference doubtful	1	1.5%	
	Totals	67 spp.	100.0%	

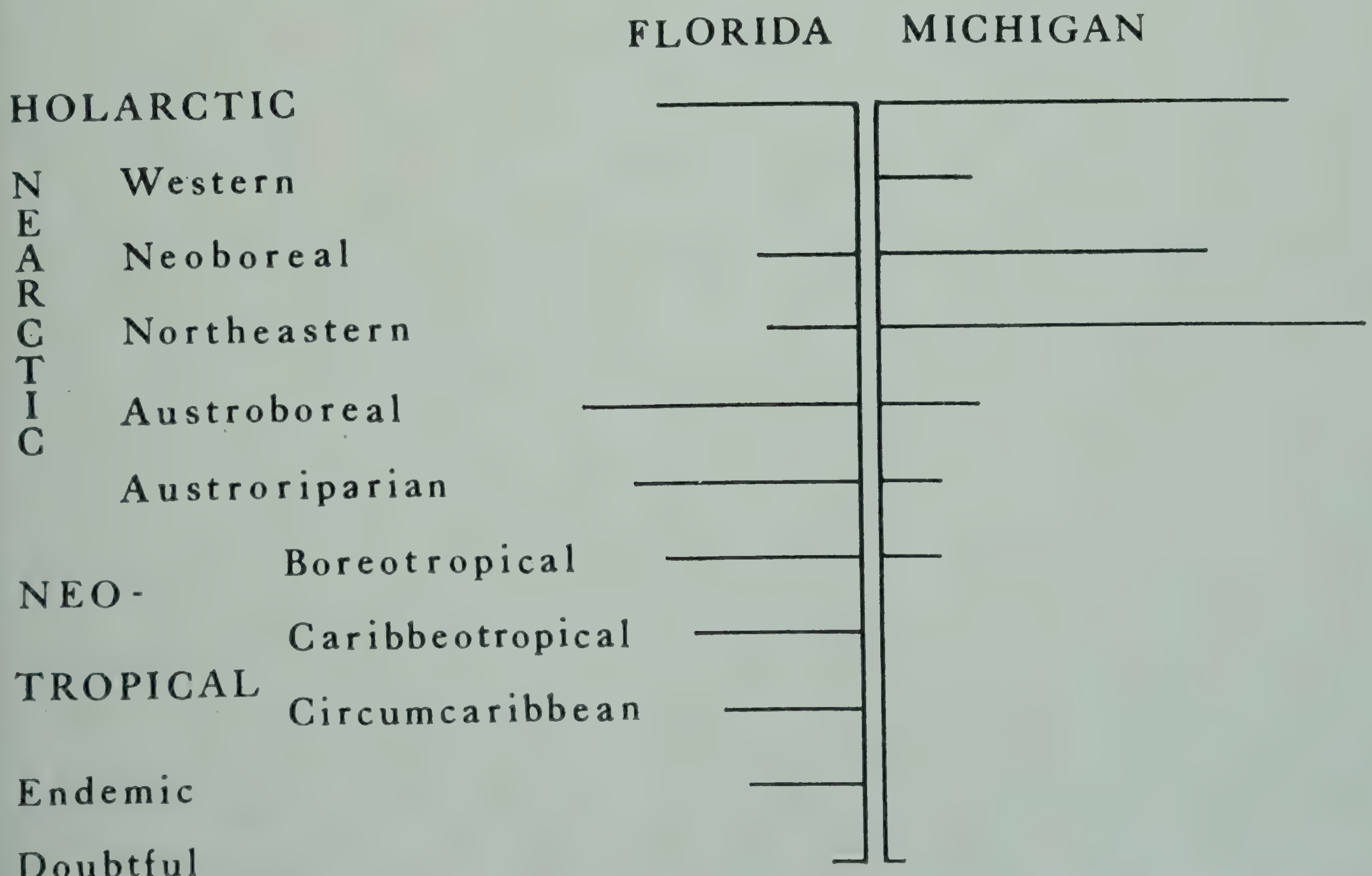


Fig. 13. Composition of ephydrid faunas of Florida and Michigan. Length of horizontal lines indicates percentage of the various categories (cf. table in text).

A fourth step was the division of the local area into smaller areas and the calculation of the composition of these areas. This was possible only in the case of Michigan, where the data is barely of sufficient amount and extent. The results shown in Figs. 14 and 15 were obtained with respect to the Holarctic and Austroboreal categories.

Extension of such a regimen as described may be of value in providing data of significance in biogeographical and phyletic studies as additional information becomes available on the Ephydridae and other taxonomic units.

LIST OF SPECIES SERVING AS BASIS FOR THE FOREGOING DISCUSSION[2]

HOLARCTIC

EPHYDRINAE: *Coenia* (*C.*) *curvicauda* (Mg.); *Ephydra riparia* Fall.; *Scatella* (*Lamproscatella*) *dichaeta* Lw.; *S.* (*L.*) *sibilans* (Hal.); *S.* (*Limnellia*) *stenhammari* (Zett.); *S.* (*S.*) *stagnalis* (Fall.); *Scatophila cribrata* (Stenh.); *S. despecta* (Hal.); NAPAEINAE: *Brachydeutera argentata* (Wlk.); *Hyadina abdominalis* (Stenh.); *H. cesta* (Hal.); *Ochthera mantis* (DeG.); *Pelina aenescens* (Stenh.); NOTIPHILINAE: *Dichaeta caudata* (Fall.); *Hydrellia griseola* (Fall.); *H. tibialis* Cr.; *Ilythea spilota* (Curtis); *Nostima picta* (Fall.); *Notiphila riparia* Mg.; PSILOPINAE: *Allotrichoma lasiocercum* Cr.; *A. trispina* Beck.; *Athyroglossa* (*A.*) *glabra* (Mg.); *A.* (*Parathyroglossa*) *ordinata* Beck.; *Discocerina* (*Diclasiopa*) *lacteipennis* (Lw.); *D.* (*Dicl.*) *obscurella* (Fall.); *D.* (*Hecamedoides*) *glaucella* (Stenh.); *Psilopa* (*P.*) *compta* (Mg.); *P.* (*P.*) *leucostoma* (Mg.); *Trimerina madizans* (Fall.).

NEOBOREAL

EPHYDRINAE: *Coenia* (*Paracoenia*) *bisetosa* Coq.; *Scatella* (*S.*) *obsoleta* Lw.; *S.* (*Philotelma*) *alaskensis* (Cr.); NAPAEINAE: *Hyadina binotata* (Cr.); *H. gravida* Lw.; *Napaea* (*N.*) *alpina* Cr.; *N.* (*N.*) *paullula* (Lw.); *N.* (*N.*) *varia* (Lw.); *N.* (*Parydra*) *bituberculata* (Lw.); *Pelina rudis* Cr.; *P. truncatula* Lw.; NOTIPHILINAE: *Hydrellia caliginosa* Cr.; *H. wilburi* Cr.; *Hydrina debilis* (Lw.); *Notiphila atripes* Cr.; *N. avia* Lw.; *N. bella* Lw.; *N. loewi* Cr.; *N. olivacea* Cr.; PSILOPINAE; *Discocerina* (*Ditrichophora*) *atrata* Cr.; *D.* (*Ditr.*) *tacoma* Cr.; *D.* (*Hydrochasma*) *buccata* (Cr.); *Psilopa* (*P.*) *olga* Cr.

NORTHEASTERN

EPHYDRINAE: *Coenia* (*Paracoenia*) *fumosalis* (Cr.); *Scatella* (*Limnellia*) *anna* (Cr.); *S.* (*S.*) *favillacea* Lw.; *S.* (*S.*) *quadrinotata* Cr.; *Setacera atrovirens* (Lw.); NAPAEINAE: *Hyadina albovenosa* Coq.; *H. bradleyi* (Cr.); *H. corona* (Cr.); *Napaea* (*Parydra*) *quadrituberculata* (Lw.); NOTIPHILINAE: *Hydrellia ascita* Cr.; *H. bergi* Cr.; *H. crassipes* Cr.; *H. cruralis* Coq.; *H. decens* Cr.; *H. formosa* Lw.; *H. ischiaca* Lw.; *H. luctuosa* Cr.; *H. penicilli* Cr.; *H. procteri* Cr.; *H. pulla* Cr.; *H. trichaeta* Cr.; *Hydrina opposita* (Lw.); *Lemnaphila scotlandae* Cr.; *Notiphila carinata* Lw.; *N. pallidipalpis* Cr.; *N. scalaris* Lw.; *N. vittata* Lw.; PSILOPINAE; *Allotrichoma atrolabris* Cr.; *A. simplex* Lw.; *Discocerina* (*Ditrichophora*) *exigua* Cr.; *D.* (*Polytrichophora*) *conciliata* Cr.; *D.* (*P.*) *orbitalis* Lw.; *Psilopa* (*Leptopsilopa*) *atrimana* (Lw.);

WESTERN

EPHYDRINAE: *Coenia* (*Paracoenia*) *turbida* Curran; NAPAEINAE: *Napaea* (*N.*) *appendiculata* (Lw.); *N.* (*N.*) *borealis* Cr.; *N.* (*Parydra*) *tibialis* (Cr.); NOTIPHILINAE: *Notiphila sicca* Cr.; PSILOPINAE: *Discocerina* (*Ditrichophora*) *montana* Cr.

AUSTROBOREAL

EPHYDRINAE: *Dimecoenia austrina* (Coq.); *D. spinosa* (Lw.); NAPAEINAE: *Hyadina furva* (Cr.); *Lipochaeta slossonae* Coq.; *Napaea* (*N.*) *breviceps* (Lw.); NOTIPHILINAE: *Nostima scutellaris* Cr.; *Paralimna decipiens* Lw.; *P. punctipennis* Wd.; *Typopsilopa atra* Lw.; PSILOPINAE: *Athyroglossa granulosa* (Cr.); *Atissa litoralis* (Cole); *Gymnopa tibialis* Cr.; *Psilopa* (*Ceropsilopa*) *coquilletti* Cr.; *P.* (*C.*) *mellipes* (Coq.).

AUSTRORIPARIAN

NAPAEINAE: *Gastrops nebulosus* Coq.; *Napaea* (*N.*) *hulli* Cr.[3]; *N.* (*N.*) *pinguis* (Wlk.); *Ochthera tuberculata* Lw.;[3] NOTIPHILINAE: *Nostima quinquenotata* Cr.; *Notiphila bispinosa* Cr., *N. furcata* (Coq.); PSILOPINAE: *Psilopa* (*P.*) *dupla* Cr.; *P.* (*P.*) *flavida* Coq.; *Ptilomyia mabelae* (Cr.); *Rhysophora robusta* Cr.

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[2] The nomenclature is that of Sturtevant and Wheeler, 1954, *Trans. Amer. Entom. Soc.* 79: 151–257.

[3] I will explain elsewhere my reasons for considering these to be distinct species, contrary to the opinions of Sturtevant and Wheeler.

CIRCUMCARIBBEAN

NAPAEINAE: *Hyadina angustata* (Cr.); *Ochthera exsculpta* Lw.; NOTIPHILINAE: *Nostima gilvipes* (Coq.); *Zeros calverti* (Cr.); PSILOPINAE: *Paratissa pollinosa* (Will.); *Psilopa* (*Ceropsilopa*) *adjuncta* Cr.

CARIBBEOTROPICAL

NOTIPHILINAE: *Nostima slossonae* Coq.; *Paralimna obscura* Will.; *Zeros fenestralis* (Cr.); PSILOPINAE: *Discocerina* (*Hydrochasma*) *incisa* (Coq.); *Plagiopsis aciculata* (Lw.); *P. skinneri* (Cr.); *Psilopa* (*Ceropsilopa*) *nasuta* Cr.; *P.* (*Leptopsilopa*) *similis* Coq.

BOREOTROPICAL

NAPAEINAE: *Ochthera cuprilineata* M. W. Wheeler; NOTIPHILINAE: *Notiphila erythrocera* Lw.; *Paralimna multipunctata* Will.; *Typopsilopa flavitarsis* Cr.; *Zeros flavipes* (Will.); PSILOPINAE: *Athyroglossa glaphyropus* Lw.; *Discocerina* (*Hydrochasma*) *leucoprocta* (Lw.); *Psilopa* (*P.*) *pulchripes* Lw.

ENDEMIC TO FLORIDA

EPHYDRINAE: *Setacera pilicornis* (Coq.); NAPAEINAE: *Napaea* (*N.*) *transversa* Cr.[4]; NOTIPHILINAE: *Hydrellia atroglauca* Coq.; *Notiphila floridensis* Cr.; *Zeros vicinus* Cr.

SPECIES OF DOUBTFUL REFERENCE

PSILOPINAE: *Discocerina* (*Diclasiopa*) *brunneonitens* Cr.; *Gymnopa bidentata* Cr.

DISCUSSION

F. G. WERNER. The maps represented show wide ranging species. Are there others with narrower ranges?

GEO. STEYSKAL. Yes, many; the maps are only selected examples.

CHARLES P. ALEXANDER. What are the number of species in Michigan and Florida?

GEO. STEYSKAL. Michigan—106; Florida—67.

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[4] I will explain elsewhere my reasons for considering these to be distinct species, contrary to the opinions of Sturtevant and Wheeler.

New Guinea and Insect Distribution

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ABSTRACT

New Guinea has played a strategic role in the spread of insects in various directions. It has functioned as an area of evolution of higher categories, and of dissemination, as well as a zone of mixture of two distinct zoogeographical regions. In a sense it has functioned as a buffer zone, isolated at different times to varying degrees. New Guinea has a distinctive insect fauna which apparently evolved in long isolation from ancient southeast Asian ancestors. During this period—perhaps over much of the Tertiary it consisted of a land mass (often called the Melanesian continent) more isolated than the present New Guinea, and centered farther to the northeast. The area may have been quite large, but probably never extended as far east as Fiji or New Caledonia, as claimed by some workers. Quite early the mass may have divided into a Solomons and a New Guinea part, each of which much later further divided. Possibly part of New Britain (except the Gazelle Peninsula), Manus Island, and the Cyclops Mountains of northcentral New Guinea are the only remaining parts of the original New Guinea portion. Southern New Ireland was apparently part of the Solomons Division. In the Pliocene much of the present high portion of New Guinea rose from sea bottom, and in the Pleistocene further elevation connected New Guinea with Australia for a sufficient period to permit exchange of the two faunae. However, the result was to give northeastern Australia more of a New Guinea fauna, and New Guinea rather limited Australian elements. These latter are largely limited to Eucalyptus *and* Melaleuca *forests in parts of southern New Guinea.*

New Guinea has exercised considerable influence on the insect fauna of the oceanic Pacific Islands, and there is evidence of this in widely separated island groups. There is a distinct depauperization in representation of higher categories with greater distance from New Guinea, with age of island groups and other factors also having their effect. In some cases, as in western Micronesia, there is also much influence from eastern Indonesia and the Philippines. There appear to be relationships between New Guinea and New Zealand, through New Caledonia, which do not involve Australia.

To date, the New Guinea fauna is insufficiently known to draw definite conclusions on many detailed aspects of this subject.

From glancing at a map of the general southwest Pacific-southeast Asia area one might tend to assume, on the basis of geographical appearance, that there would be a general gradation of zoogeographical relationship, from one island group to the next, in passing from southeast Asia, through Indonesia, to New Guinea, Australia, and the islands of the southern Pacific. For in many parts of the world reasonable deductions can often be made that adjacent areas may be similar in fauna, and that the fauna of a mountain area may be similar to that at a lower altitude some distance away, while progressing farther from the equator, likewise that isolated mountain masses of similar latitude may possess elements in common—often archaic remnants of former widespread types since confined to the higher areas by climatic change, or invasion of the sea, or gradual migration under changing circumstances, resulting in extinction in the lower intervening areas. However, as the fauna of New Guinea and nearby islands becomes better known, a number of striking and puzzling facts confront us. Unfortunately, the knowledge of the insect fauna of this area is still at such an early stage that firm conclusions cannot be drawn. As a matter of fact, some strongly contradictory views are held by different workers. Of course, it is quite true that different relationships and distribution patterns are manifested by different groups of insects with different evolutionary histories, or different habits and different methods of dispersal. And the geological history of the area is apparently such that development or spread in different periods of time could have profoundly affected the nature of contemporary distribution. On the other hand, the collections which have been studied for the area have been of such uneven geographical representation, and so incomplete, that different conclusions have necessarily resulted from the work of taxonomists studying particular collections.

That different groups present different patterns is conspicuously emphasized by different geographic relationships between insects in general on one hand and higher vertebrates on the other. For the mammal fauna of New Guinea is to a considerable degree Australian, whereas though early workers assumed that the same relationship applied to insects, more and more studies are showing this not to be so in general. The native mammals of New Guinea are entirely marsupials, monotremes, rodents and bats. Thus they are all animals which could have migrated over a land connection from Australia or whose ancestors might have come by "island hopping" from the west. In western Indonesia, southeast Asia and in the Philippines there are nine orders of mammals—insectivores, pangolins, flying lemurs, primates, carnivores, lagomorphs, proboscideans, artiodactyls and perissodactyls none of which are represented in New Guinea. Only a few species of these groups are found in the Celebes area, and marsupials extend westward to Celebes. When Wallace (1869) crossed over from western Indonesia to Celebes he noticed the very great contrast in many forms of life between the two areas. The line he drew dividing the archipelago was later called "Wallace's Line". Though later study of some groups has shown that the contrast was not quite as great as assumed by Wallace, nevertheless the line does have considerable significance and forms the boundary line of the generic ranges of many insects. Furthermore the number of genera represented just west of the line is very much greater than just east of the line. Thus it represents a barrier of long standing both to eastward and westward migration. The Philippines, however, though possessing much in common with Borneo, nevertheless likewise have considerable in common with "Wallacea" and the New Guinea area. The suggestion has been made (Gressitt, 1956a) of a diversion or forking of the line to go between Borneo and most of the Philippines, following Dickerson *et al.* (1928) and others. Furthermore, there are a number of genera or tribes common to the Philippines and New Guinea area which are absent from, or hardly represented in Celebes.

These circumstances suggest that New Guinea has had some connection with the Philippines through the Moluccas, at least in part independant from Celebes, but at quite ancient periods. As shown by Karny (1929), Toxopeus (1950), and others, the insect fauna of New Guinea is basically of ancient Asian origin, with only recent invasion from Australia. (See Lam. 1934, for similar view regarding the flora). Any direct Asian connections must have preceded the Tertiary or much of it and antedated the spread of higher mammals. The connection could have been later than the development and spread of marsupials, as these became extinct west of the old Wallace Line from competition with higher mammals. As the Philippines and New Guinea on one hand and the Philippines and Borneo on the other hand, have relatively more in common with each other than have Borneo and Celebes, it seems likely that the early connections of New Guinea were with Asia through the Moluccas, Philippines and Borneo. Celebes has evidently been isolated for a very long period, and has a number of endemic genera, besides absence of many genera found in the nearby areas. Although somewhat of a mixing zone, it must have once been smaller and more isolated from neighboring areas, particularly from Borneo. The sea separating Celebes from Borneo, though not very wide, is very deep, giving added evidence of long isolation. The geological history of the eastern Indonesian area has apparently been very complicated, with much rising and falling, so that at different periods there have been various temporary partial land bridges or stepping stones, permitting partial faunal mixture. Australia has apparently had little direct influence, except for Timor.

I have already cited evidence (1956a) for the relationship of the New Guinea fauna with that of the Philippines, on the basis of the distribution of several conspicuous groups of beetles. Toxopeus (1950) has stressed the general Malayan relationships of the New Guinea butterflies, stating that Australia has had only a minor influence except in southeastern New Guinea.

In attempting to explain the origin of faunae of oceanic islands, we conclude that most of the immigration has been by means of transport in air currents. One might then ask if such transport is not constantly occurring from rich continental areas to nearby continental islands, or from one large continental island to another, particularly since most of these we are considering are relatively much closer to each other than are many of the oceanic islands to their supposed faunal source areas. In view of the distinct identity of the faunae of some of these continental islands, presumably the answer may be that such immigrants to rich continental areas rarely have the chance to establish because of the rigorous competition, predation or parasitism, they encounter in a rich harmonic fauna, whereas on an oceanic island with highly disharmonic fauna they are likely to find themselves in an empty ecological niche, or at least encountering few competitors, predators or parasites. To be sure such introductions to continental islands must take place, and possibly actual continuous land connections were not as complete as supposed. On the other hand, the distinctness of the Celebes fauna, in the light of its proximity to Borneo, seems to argue that aerial migration has played a minor role in contributing to the faunae of these old continental islands.

Even with continental islands, of course, we must distinguish categories on the basis of length of isolation, for New Guinea presents a quite different situation from that of Borneo. Though continental, the New Guinea fauna has been inherited from ancient, and later temporary, connections, and is not a fully harmonic or true continental fauna, in spite of being so rich. In that sense also, to be sure, the rich Australian fauna, and more so that of New Zealand, is not fully harmonic, for some major categories of insects are lacking, as well as many important groups of higher vertebrates. Speaking of the Papuan Subregion (Moluccas to the Solomons and Cape York Peninsula), the area possesses a very large number of endemic genera, as with a well isolated group of old oceanic islands, or a continent. Borneo, on the other hand, with its tremendous number of genera, has very many of them in common with Sumatra and southeast Asia. The Papuan Subregion is thus a very distinct subregion, whereas the Philippine Subregion is less distinctive, and the Malayan Subregion tends to merge with the Philippine and Indo-Chinese subregions.

In speaking of the age and long isolation of the New Guinea fauna, we must bear in mind that much of New Guinea is extremely young geologically. It is said that the high ranges extending east and west along the axis of the island are partly among the youngest in the world, and that these were elevated from shallow sea bottom only in the Miocene and Pliocene periods, even to the end of the latter. Then with the Pleistocene ice age sea level recessions, the new southern part of New Guinea came in contact with northeastern Australia across the shallow Torres Straits, and the faunal exchange took place. Apparently parts of eastern New Guinea and part of the north coast area such as the Cyclops Mountains near Hollandia are of very much greater age (Cheesman, 1951). Some of these mountains have been stated to have been continuously above water since pre-Cambrian times.

The ancient true New Guinea fauna must have developed on the so-called "Melanesian continent", formerly situated just to the north of the present New Guinea. Probably Manus Island and the Cyclops Mountains, and the Solomon Islands, are remnants of this ancient continent. We shall return to that subject in a moment.

There is much evidence, geological and biological, for the youth of much of New Guinea. The coral limestone found at many of the high altitude areas can be rather accurately dated. Erosion patterns, changes in river routes, rivers passing through later raised mountain ranges, and many other phenomena are demonstrative. In the Wisselmeren area of western Netherlands New Guinea, just west of the Snow Mountains, recent changes are quite obvious. Of this group of four lakes, one (Kamo Valley) has become a great stretch of marsh and swamp, the latter supporting some spreading forests. Another (Paniai) is being invaded by marshes, as rivers drain in from the Snow Mountains, and with the recent change in outlet draining to the south coast instead of to the north coast as it formerly did. The earlier outlet has left a deep canyon cut from the former edge of the lake, which latter is now nearly 50 meters in altitude above the present lake surface. Earthquakes are frequent here. One the year before my visit partly changed the course of a stream entering the lake. Toxopeus (1950) describes other evidence of geologic youth in the area where he worked in the Snow Mountains.

On the south side of the Snow Mountains is a cliff over 3,000 meters high, the highest in the world, said to have resulted from the snapping of rock masses in relieving crustal stress, with a differential movement on the two sides of the fault. Much of the old rock structures are exceedingly tilted and folded. These crustal movements took place in Pliocene times, say two or three million years ago (Hodge-Smith). This can be compared with the last major crustal deformations in Australia which are said to have died out in the Carboniferous, about 250 million years ago. About 40 years ago there was a subsidence of two meters along the coast at Aitape, northern New Guinea. Along much of the north coast there are strongly meandering rivers, extensive swamps, and often very low narrow beaches, indicating stress.

Many of the high mountain ranges in eastern New Guinea such as the Bismarcks and related ranges and the Owen Stanley Range, are of great geological age, even consisting of pre-Cambrian schists and gneisses, but have been raised and lowered at different periods. Much of the time they have formed islands, as have other New Guinea ranges up into the Pliocene. This archipelagoan nature of New Guinea through much of the later Tertiary contributed to the development of local endemism, which has been perpetuated in the mountain ranges since the islands were united. With the various earlier periods of subsidence of these islands, limestone beds were laid down, which now may be found high in the mountains. In the west they completely cover the old metamorphic rocks. There are many intrusions of granite and diorites. Vulcanism and lava outpouring continued through the Tertiary, on down to the present time. During the periods of Pleistocene glaciation there were glaciers extending down to altitudes of less than 3,000 meters.

Most of the fossils found are marine deposits, often coralline or forminiferal limestones, or sandstones or mudstones containing marine shells. Some of the Pleistocene rocks contain fossil emu and cassowary bones, or those of the extinct *Nototherium*, a large rhinoceros-like marsupial.

As pointed out by Toxopeus (1950) New Guinea does not possess a true alpine fauna. This is in spite of New Guinea having one of the world's highest mountain ranges, with conditions favorable for life, and plants growing up to nearly 5,000 meters in altitude. This strongly suggests that the connections of New Guinea with other areas existed at low altitudes preventing high altitude forms from reaching the island. There are no coniferous forests in the very high mountains, the conifers being mainly auracarians, podocarps, and cupressines, occurring at medium or even fairly low altitudes. The insect fauna of the high altitudes represents a recent development, of lowland forms adapting themselves to a cooler climate. At the highest altitudes butterflies are rare or absent, and those reaching high altitudes belong to the same genera as those occurring much lower down. Though Darlington (1952) has described considerable neoendemism on the generic level in carabid beetles for the Mt. Wilhelm area, in some other groups there is not a great deal of local generic endemism. Many of the strictly Papuan genera may be widespread within New Guinea.

At 3600 meters altitude on Mt. Wilhelm I collected local species of the dominant Papuan longicorn genus *Tmesisternus*. This genus is represented by many species at sea level. In Toxopeus' collection there are likewise endemics from the Snow Mountains in this genus. Other cerambycids are also represented by different species within the same genus from sea level to fairly high altitudes. Among the hispine beetles, the highest collections made, at just under 2,000 meters, both in western and eastern New Guinea, represented a genus, *Brontispa*, found predominently at sea level. Although *Troides* (*Ornithoptera*) butterflies are characteristic of the lowlands, I found the chrysalis of one species at close to 2,000 meters altitude (Gressitt 1956b).

In a rough comparison of material I collected at similar altitudes in the mountains of eastern and western New Guinea, 1,000 kilometers apart, definite differences in faunal make-up were noticed. For instance, broad-nosed weevils were dominant in the highlands of the northeast, and cryptorhynchine weevils were dominant in the Wisselmeren area. Also, more types familiar in southeast Asia were noticed in the latter area, both of insects and plants. In general, more species of cerambycids were taken at lower altitudes, and more chrysomelids at higher altitudes, but this may have been partly a matter of favourable environments and unequal sampling. In the more densely populated mountains, there is more cleared land, favoring shrubs and herbs, and thus likewise favoring the leaf beetles.

In the lowlands, a single species may extend very great distances, as all the way from Waigeo Island at the far northwestern end of New Guinea, along the north coast far into eastern Papua (Gressitt, 1955). On the other hand in the mountains there is great development of local species endemism.

The extent of representation of true Australian groups in New Guinea obviously varies considerably, as suggested in connection with the Australian nature of the mammal fauna. Certainly for many groups of insects (Lieftinck, Karny, Toxopeus) the New Guinea fauna is Australian only to a minor degree. In the Cerambycidae and Chrysomelidae the percentage of genera in common between New Guinea and Australia south of the Cape York Peninsula is very low. A few of the Australian genera are widespread in New Guinea, but others are limited to the southeastern portion, as are, to a large extent, the *Eucalyptus* and *Melaleuca* savanna forests. The evidence in the beetles I have studied strongly suggests that much of the faunal representation on the Cape York Peninsula is of Papuan origin, particularly that found in the rain forests. This suggests that previous to the Pleistocene connection there may not have been much of a locally developed rain forest flora and fauna in that area, or that the invading Papuan biota was better adapted to the climate of the area. Also that the Australian insect forms invading New Guinea encountered the competition of a fairly rich and balanced fauna, which was not the case with the mammals. The typical Australian forms are largely limited to the *Eucalyptus* savanna, just as they are in New Guinea. In the hispines, the genus *Eurispa*, the only large Australian genus in the subfamily, barely extends into southeastern New Guinea, with two known forms, besides a few on the Cape York Peninsula. In the rain forests of Cape York Peninsula the hispine are represented entirely by typical New Guinea genera, which in some cases extend all the way to Indonesia. Toxopeus (1950) points to a secondary invasion of Papuan types to the Cape York Peninsula through the Aru-Merauke ridge, from the direction of the southern Moluccas. According to some geologists New Guinea was also connected with Australia in the Paleozoic. If so, the connection must have had very little permanent effect on the fauna as a result of later submersions or ecological incompatibility of the Australian fauna with the New Guinea environment.

The old Melanesian continent, on which evolved many of the typical Papuan genera, apparently divided into two major islands at some period of the Tertiary before the Pliocene. The west division then developed the particular New Guinea elements, partly before breaking up into the various islands which developed more local endemism, now perpetuated in various of the mountain ranges of New Guinea. The eastern division of the Melanesian continent gave rise to the Solomon Island fauna. New Guinea is said to have consisted of two major islands, the east and west portions, during part of the Pliocene, but were connected both earlier and later. The Solomon Islands, at least in part, appear to have been individually isolated from each other for a considerable period, perhaps at least since well back into the Pliocene. Evidence for this includes the fairly deep water between many of the major islands, and the considerable development of endemism for single islands, or parts of the chain. Probably some of the islands of the Solomons have been separated from each other longer than have parts of the Bismarck Archipelago from the New Guinea mainland.

New Ireland holds an interesting position in the relationship of the supposed two major divisions of the old Melanesian continent. For in spite of its proximity to New Britain and others of the Bismarcks, it has a number of elements in common with the Solomons. Southern New Ireland has ancient metamorphic rocks well in evidence, whereas most of New Britain consists of raised marine limestone or recent volcanic deposits, at least on top of the older rocks. The New Ireland population of the birdwing *Troides priamus d'urvillianus* is blue like those of the Solomons, instead of green like the New Britain population. In my collecting in southern New Ireland a few weeks ago I took a new hispine beetle related to a form described as an endemic genus from Malaita (latter also occurring on Guadalcanal). Another species on Manus Island may be a connecting link between this genus and one restricted to New Guinea and Waigeo, though showing its next closest affinity in Madagascar. Another form just taken in New Ireland seems to represent a new genus without known close affinity in the Solomons or New Guinea, but having a general similarity to some Philippine forms. Still another seems to have its closest affinity in New Britain. But with many of the common insects taken in southern New Ireland, there appeared to be more affinity with species of Bougainville than with those of New Britain.

It can be noticed that the Solomon Islands are principally arranged in two parallel rows, which appear to unite at each end, in Bougainville and San Cristobal, respectively. It has been stated that southern New Ireland represents a continuation of the southern chain of the Solomons, and that the several small islands paralleling New Ireland on the northeast represent the continuation of the north chain of the Solomons. Not enough collecting has been done to present much evidence on this point, or to adequately characterize the relationships of New Ireland, New Hanover, the St. Matthias group, Manus, and New Britain. At any rate, New Britain has much in common with the New Guinea mainland, although plenty of local species endemism. Possibly Manus is a little less closely similar in its fauna to New Guinea, than New Britain is to New Guinea.

The submarine land connections in the Solomons (Lever, 1937) show that Bougainville connects with the Shortlands, Choiseul, Ysabel, Nggela, Russell Islands, and Guadalcanal, shallower than the 1200 meter line, whereas the New Georgia group, Malaita and San Cristobal are each isolated by water from 1200 to 2000 meters in depth. Further, Rennell and Bellona are separated from the rest of the Solomons by water more than 4,000 meters deep. In my recent collecting on Bougainville and Guadalcanal, I noted many common types on the two islands that superficially appeared to be very similar or identical, as might be suggested by these ocean depths. However, in the hispines, of six kinds taken on Bougainville and 11 on Guadalcanal, only two on each represent close relationships, and one of these is a widespread coconut pest. Some of the others represent new genera, for the time being endemic to one or the other of the two islands. Some were found on one island in ecologic niches which seemed to be vacant on the other, and vice versa. Mr. E. S. Brown (personal communication) tells me that in his recent collecting, he noted that Malaita appears to have a very rich fauna, with some types he did not note on Guadalcanal, and that the fauna of San Cristobal appears still more distinct, though not as rich. Within the New Georgia group there is some distinct local speciation (Mayr, 1932; Lever, 1953), with several of the various islands having endemic species. In spite of close proximity, some of the water separating these islands is a few hundred fathoms deep. Much of the rocks on the main Solomons are igneous, and many of them may date from the Cretaceous Period. Limestone terraces indicate that there has been elevation in recent times. Rennell Island, which stands apart from the double chain, is a raised atoll. It has a rather distinct, though poorer, fauna.

When the faunae of the Solomons, Bismarcks and New Guinea are better known, it will be very interesting to compare the nature of speciation on these now isolated islands, with that on the mountain ranges of the New Guinea mainland, since the latter are said to have been, to a great extent, isolated islands in the late Tertiary.

The fauna of the New Hebrides is still less adequately known, but the apparent much greater poverty, and lack of many groups found in the Solomons has lead some (Mayr, 1941; Gressitt, 1956a) to call these islands oceanic. Others, however, have classified not only the New Hebrides, but also Fiji and New Caledonia, or even Samoa, as continental islands.

New Caledonia appears to represent a relic of a possibly important phase in the history of the New Guinea fauna. Karny (1929), Malaise (1950), and others, have pointed out South American relationships in the New Guinea insect fauna. There is much evidence of faunal relationships between New Guinea and New Caledonia, and again between New Caledonia and New Zealand (Gressitt, 1956a). Many of these relationships do not involve Australia, and it seems to be a rather safe assumption that the New Guinea—South American relationships may stem from connections through the Solomons, New Caledonia, New Zealand, and Antarctica, completely independent of Australia, in addition to other connections which may have existed between Australia and South America. New Caledonia has very ancient rocks, with much serpentine. Its fauna and flora possess a very high percentage of both specific and generic endemism.

Lord Howe Island, off the east coast of Australia, is also significant from the standpoint of zoogeography in this area. It possesses a number of endemic forms without relatives in Australia, or with no relatives in Australia south of the Cape York Peninsula. This suggests that its fauna may have been derived from islands to the north. Some of the Lord Howe forms represent the southernmost extent for particular genera. The island lacks many dominant types of insects found in New Zealand and Australia. The flora, as well as the insect fauna, indicates a more tropical derivation, for there are four endemic species of palms on the island.

The Papuan Subregion has exercised a great influence on the insect fauna of Polynesia (Mayr, 1941; Gressitt, 1956). Briefly, the bulk of the Polynesian fauna may be said to have been derived from the Indonesian-Philippine-New Guinea areas, with New Guinea having a particularly strong influence in eastern Melanesia and central Polynesia, but with more Philippine influence in western Micronesia (Gressitt, 1954).

Many of the above statements are based on incomplete evidence, and much study of the insect fauna of the Papuan Subregion is necessary before the insect zoogeography of this area is fully clarified.

REFERENCES

Cheesman, L. E. 1951. Old mountains of New Guinea. *Nature* 168: 597.

Darlington, P. J. 1952. The carabid beetles of New Guinea. Part 2. The Agonini. *Bull. Mus Comp. Zool.* 107 (3): 89–252, map, 4 pls.

Dickerson, R. E., E. D. Merrill, *et al.* 1928. Distribution of life in the Philippines. *Monogr. Bur. Sci. Manila* 21: 1–322, 64 text figs., 43 pls.

Gressitt, J. L. 1954. Introduction. Insects of Micronesia (B. P. Bishop Mus.) 1: 1–257, map, 70 figs.

Gressitt, J. L. 1955. The longicorn genus *Tethionea* (Coleoptera: Cerambycidae). *Proc. Hawaiian Ent. Soc.* 15 (3): 411–417, 21 figs.

Gressitt, J. L. 1956a. Some distribution patterns of Pacific island faunae. *Syst. Zool.* 5 (1): 11–32, 47, 9 maps.

Gressitt, J. L. 1956b. Entomological investigations in New Guinea mountains. *Proc. Hawaiian Ent. Soc.* 16 (1): 47–69, 10 figs.

Hodge-Smith, T. 1943. The geology of New Guinea. *The Australian Mus. Mag.* 8 (3): 91–95, 4 figs.

Karny, H. H. 1929. On the geographical distribution of the Pacific gryllacrids. *Proc. Fourth Pac. Sci. Congr.* 3: 157–172, 6 maps.

Lam, H. J. 1934. Materials towards a study of the flora of the island of New Guinea. *Blumea* 1: 115–159, 3 maps.

Lever, R. J. A. W. 1937. The physical environment, fauna and agriculture of the British Solomon Islands. *Tropical Agriculture*, Trinidad 14 (10): 281–285, 14 (11): 307–312, 4 figs., 2 maps.

Lever, R. J. A. W. 1953. Faunal speciation in New Georgia, Solomon Islands. *Pacific Science* 7 (2): 250–251, 1 map.

Lieftinck, M. A. 1942. The dragonflies (Odonata) of New Guinea and neighbouring islands, VI. *Treubia* 18 (3): 441–608, 2 figs., 19 pls.

Malaise, R. 1950. New entomological evidences of a former trans-Pacific land-connection. *Proc. Eighth Int. Congr. Ent.*, Stockholm: 434–437.

Mayr. Earnst. 1932. Birds collected during the Whitney South Sea Expedition, XX. *Amer. Mus. Novitates* 522: 1–22.

Mayr, Ernst. 1941. Borders and subdivisions of the Polynesian Region based on our knowledge of the distribution of the birds. *Proc. Sixth Pacific Sci. Congr.*, Berkeley 4: 191–195.

Toxopeus, L. J. 1950. The geological principles of species evolution in New Guinea. (A study on parallelisms in geological and lepidopterological development). *Proc. Eighth Int. Congr. Ent.*, Stockholm: 508–522, 3 maps, 7 figs.

Wallace, A. R. 1869. The Malay Archipelago. *MacMillan and Co.* Maps and illustr.

High Altitude Insects of the Himalayas

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ABSTRACT

High altitude insects of the Himalayas are of interest from several points of view. Very little is known of the insect fauna of the Himalayas, especially of the denizens of high altitudes. The nature of adaptations of various species to the abnormal conditions of life prevailing at high altitudes is little understood. From the point of zoogeography and because of the geographical location and varied climatic conditions of the Himalayas, it is of interest to know whether the fauna is of palaearctic or of oriental origin.

This paper gives an account of the observations made in the North West Himalayas, especially at the higher altitudes between 8,000 ft. and 15,000 ft., in the Kulu, Lahaul, and Spiti Valleys, in the Panjab (India) during the summer of 1955. General ecological conditions of the places visited are recorded and the life of the insects at high altitude, especially those associated with soil and vegetation, in streams and rivers and on the vast snow field at the Rohtang Pass, is described. The following general conclusions are drawn from these observations subject to the limitations of the identified material. There is a general reduction in the number of species, although the number of individuals or populations of a species may be quite large. Most of the insects were associated with life in soil, chiefly in sheltered condition near rocks or under stones, or with water in glacial streams and rivers. Owing to the preponderance of torrential streams at high altitudes, the aquatic insects were chiefly adapted to this environment. In general the species showed remarkable increase of black or dark pigmentation. An increase in hairiness was observed in certain other forms. Partial or total reduction of wings in different Coleoptera and Heteroptera was also commonly observed in populations living at about 10,000 ft. and above, but not normally at lower altitudes.

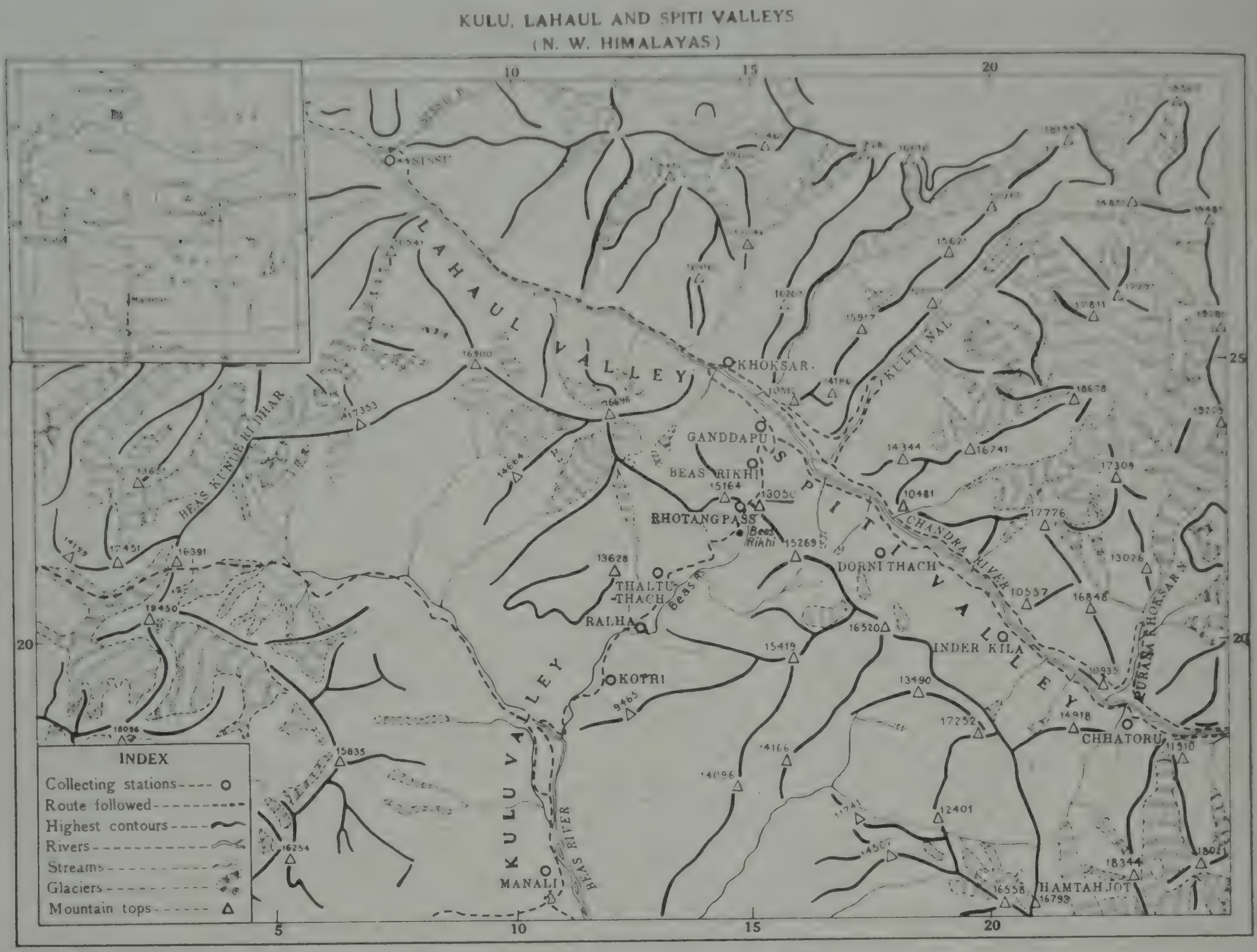
The genera found were mostly palaearctic or holarctic in distribution, and only rarely of oriental origin. As far as known they were widely distributed also in other parts of the Himalayas. The species appeared to be mostly endemic to the Himalayas.

INTRODUCTION

In the Himalayas there is a wide range of climate, vegetation and animal life. While the plants and animals occurring at relatively lower altitude are better known, the insects of the higher altitudes are inadequately known.

The present paper offers an account of the observations made in May and June 1955, on the insect life at altitudes between 5,000 ft. and 15,000 ft., of the Kulu, Lahaul and Spiti Valleys (Map 1) in the N.W. Himalayas sometimes known as the Panjab Himalaya. It lies at a slightly higher northern latitude and is characterised by a number of widely separated parallel ranges, such as the Siwaliks, the Dhola Dhar, the Pir Panjal, etc. Here the mountain peaks are not as high as in the eastern Himalaya, the greatest height being a little less than 23,000 ft. above the sea-level. The rain fall is also scanty and the line of tree-growth runs along contours of 10,000 ft. to 12,000 ft. compared to some 15,000 ft. in the eastern Himalaya. The permanent snow line, likewise, runs a few thousand feet higher than the line of tree-growth. In most other characters, however, the N. W. Himalaya is similar to the rest of the Himalayas. From the entomological point of view, only a fraction of these parts have been investigated but from the results obtained from the journies of Herr C. F. Hűgel (1844) in Kashmir, and of M. Guy Babault (1922) in N.W. India, it was evident since a long time that these parts of the Himalayas were full of great entomological interest. In recent years further attempts have been made in India to investigate the insect fauna of these parts and the present account refers to one such attempt made in conjunction with a party from the School of Entomology, St. John's College, Agra. The account, however, refers mainly to my own observations and collections comprising over 5,000 examples. The accompanying map shows the places that were visited in the Kulu, Lahaul and Spiti Valleys, situated in the Kulu Subdivision of the Panjab (India).

Our trek commenced from Manali, (32°, 15′N. 77°, 11′E.) *Ca.* 6,000 ft. above sea-level, in the Kulu Valley and roughly took the shape of *T* with the Rohtang Pass (32°, 22.5'N. 77°, 15'E.), Ca. 14,000 ft., as the meeting point of the Kulu Valley in the South and the Lahaul and Spiti Valleys in the north.


KULU, LAHAUL AND SPITI VALLEYS
(N. W. HIMALAYAS)
LAHAUL VALLEY
SPITI VALLEY
KULU VALLEY
CHANDRA RIVER
BEAS RIVER
BEAS KINNE KIDHAR
KULTI NAL
PURANA KHOKSAR
KHOKSAR
GANDDAPU
BEAS RIKHI
ROHTANG PASS
Beas Rikhi
DORNI THACH
THALTU THACH
RALHA
KOTHI
INDER KILA
CHHATORU
HAMTAH JOT
MANALI
SISSU
INDEX
Collecting stations
Route followed
Highest contours
Rivers
Streams
Glaciers
Mountain tops
5
10
15
20
25

Map 1. Map of the Kulu, Lahaul and Spiti Valleys showing the parts surveyed during May and June, 1955.

GENERAL ECOLOGICAL CONDITIONS

The cultivated area of the Kulu Valley is less than 7 per cent of the total area. The remainder consists of mostly the forests, grasslands and desolate mountain waste above the limits of tree-growth. Highest villages are situated in the neighbourhood of 8,000 ft. and are usually surrounded by terraced fields where rice, wheat, barley, maize, potato, etc., are cultivated depending upon the suitability of land and climatic factors. Planted here and there in the villages and in the fields are the apricot, plum, walnut and the evergreen oaks (*Quercus semicarpifolia and Q. dilatata*) the leaves of which serve as fodder. Slopes of steep grass and strips of coniferous forests separate the different villages. Higher up, depending on the availability of soil and favourable aspect of the mountains, the silver fir (*Abies pindrow*) with patches of maple (*Acer caesium*) or the Indian horse-chestnut (*Aesculus indica*) are to be seen. These are succeeded in turn at higher elevations by woods of stunted oak (*Quercus incana*), birch (*Butula utilis*) and Rhododendron (*R. campanulatum* and *R. arboreum*).

Unlike the case in parts of eastern Himalayas where the streams and rivulets are fed by rains, here the main source of water is the melting snow and glaciers and the permanent springs because, owing to the absence of monsoons, the rains are scanty. In summer the whole scenery is crowned by rounded grassy summits, the apparently bare ridges of rocks and the tops of the great ranges capped with perpetual snow. In winter, on the other hand, the ground is covered with snow which may last from a few days to several months, depending upon the locality, but it does not last long at heights of less than 6,000 ft.

As we go higher up the conditions of life become severe; the rigours of climate and the relative scarcity of food make these areas increasingly inhospitable. The temperature, humidity and atmospheric pressure decrease. For hours together, during day or night, fierce winds blow in different directions, but often with a regularity. Over wide areas covered by snow there is usually a fierce display of light and glare. When the sky is clear, the bare rocks become considerably heated in spite of the low atmospheric temperature. The nights are bitterly cold and there is a great fluctuation of temperatures in the day and at night.

However, what might appear a barren landscape, is really not quite so when examined closely. The older rocks and boulders are covered by lichen and moss which eventually break them up and build the soil and accumulate humus in the narrow spaces between rocks. One also comes across grass and typically dwarf perennials with hard, woody roots. In a short active season their flowers rapidly bloom, and as rapidly fade away. Such places form the niches with microclimate of their own and afford home or shelter to a variety of insects, spiders and centipedes. Another but similar kind of niche is provided by the narrow spaces under stones and boulders. These are also usually rich in humus. All these places are no doubt under snow for a great part of the year, but probably because the temperature there is more equable and the spaces more sheltered against the howling winds, the different forms of life are attracted there for shelter or abode.

INSECT LIFE AT HIGH ALTITUDE

With the present state of our knowledge I find it rather difficult to give a clear-cut definition of what may constitute "high altitude". The definition would, it seems, vary according to the geographical location. Although we collected insects at altitude between 5,000 ft. and 15,000 ft., preliminary observations showed that most of the species that were collected at 12,000 ft. and above, would only rarely be found at lower than 8,000 ft., and also in relatively smaller numbers. Further collecting and study of the species would no doubt be necessary, but for the purpose of the present paper we may refer chiefly to the collections made at 9,000 ft. and above, except in certain cases of more widely distributed species.

Insects Associated with Soil and Vegetation

The forficulid (Dermaptera), *Anechura bipunctata zubovskii* Sem., was collected in fairly large number from under stones in meadows, near river banks and on the periphery of forests at various altitudes between 9,000 ft. and 13,000 ft., namely from Ralha (9,000—12,000 ft.), and Thaltu Thach (11,800 ft.) in the Kulu Valley and from Ganddapu (11,000 ft.) to as far west as Purana Khoksar Nal (13,000 ft.) in the Spiti Valley. At that time the females had laid eggs, and were guarding these at lower altitudes, but not so at the higher altitudes. Burr (1910) records this sub-species from various localities in Kashmir generally between 8,300 ft. and 10,000 ft., with one exception from Scinde Valley at 7,000 ft. Another forficulid, *Oreasiobia stoliczkai* (Burr), of which many examples were collected from Sissu (10,500 ft.) and Khoksar (10,800 ft.) in the Lahaul Valley, and the rest from the Kulu Valley, mainly from Ralha (*Ca.* 9,000 ft.) with the exception of 3 examples from Kothi (8,000 ft.) and Manali (6,000 ft.). The species was originally described from the Upper Sutlej District in Northern India, and at the time of our visit in the two valleys mentioned above, a large number of larval forms were seen. *Forficula beelzebub* (Burr), which is a widely distributed species in the eastern Himalayas (Nepal, Sikkim, Assam), was obtained from Manali (6,000 ft.) but not from any higher altitude. It is a species with lighter colour than the previous two species which are dark.

Beetles (Coleoptera) were perhaps the most numerous and varied of all the insects collected. The ground beetles, Carabidae, from these parts have already been reported upon by Andrewes (1924) who studied the collections made by M. Guy Babault. *Calosoma maderae* var. *indicum* Hope and var. *kashmirense* Bruen. were collected at various altitudes between 6,000 ft. (at Manali) to 11,800 ft. (at Thaltu Thach). *Chaetobraoscus anomalus* (Chaud.), which is an apterous species was collected in fair numbers from under stones at the Rohtang Pass (14,000 ft.), Chhatoru (11,800 ft.) and Purana Khoksar Nal (13,000 ft.). It is black in colour like most other species of beetles from high altitudes. Over six species of *Bembidion*, a cosmopolitan genus, were collected; but of these only two species, *B. gagates* Andr. and an apparently undescribed species of *Bembidion*, have a wide range of distribution, having been obtained from between 6,000 ft. (only a few examples) to 11,000 ft. *B. gagates* has also been stated by Andrewes (1935; p. 142) to be common throughout the western Himalayas up to 10,000 ft.

Trechus thibetanus Jeann., previously known from Sikkim in the eastern Himalayas and from Tibet, was obtained from 12,000 ft. to 12,500 ft., near the source of Beas river, a couple of miles north of Ralha in the Kulu Valley. This is also an apterous species, examples of which were collected from 17,000 ft. by the Third Mount Everest Expedition; this height, according to Andrewes (1935, p. 73), "is probably the highest where Coleoptera have ever been met with." *Agonum* (*Oxypselaphus*) *lissopterus* Chaud. and *A.* (*Anchomenus*) *caesitium* Andr., are other species which were taken in long series at various localities between 11,000—13,000 ft. with the exception of a few examples of the latter from 10,000 ft., and of the former from 13,800 ft. Again, both these species are wingless and are of shining black or dark blue colour. Here we may also refer to other apterous species of Carabidae collected: an undetermined species of *Agonum* was collected from Ganddapu (11,000 ft.) at the base of the Rohtang Pass; *Calathus himalayae* (Bates), and another species of the same genus were taken from 11,000—12,000 ft. on either side of the Rohtang Pass; an apparently undescribed species of *Nebria*, which is also apterous and shining dark blue in colour, was taken from snow at 14,000—14,200 ft., on the Rohtang Pass.

Certain other species of Carabidae were found to be more widely distributed. Of these the ones taken in long to fairly long series may be mentioned. *Bradtus batesi* Csiki, *Harpalus melaneus* Bates, *H. lepcha* Andr., *Amara darjelingensis* Putz. and *Calathus kollari* Putz., are all winged species and were taken at various stations with altitudes between 6,000—12,000 ft.

Next perhaps only to Carabidae, the species of Staphylinidae collected were quite numerous. These were collected mostly from ground, from beneath stones and from damp edges of streams and pools. Much of this material still awaits identification, but some that has been determined may be referred to here. *Staphylinus* (*Pseudocypus*) *almorensis* Camer., hitherto known from the Kumaon Hills and Trium in the Punjab, at 9,000—9,300 ft., was collected from Dhorni Thach (11,800—12,000 ft.) and Chhatoru (11,000 ft.) in the Spiti Valley but not from the Kulu Valley. Three other species of the same genus were, however, obtained in small numbers from the latter valley, between 6,000 ft. and 9,000 ft. *Coprophilus* (*Zonoptilus*) *burphuensis* Champ., which is previously known from the Gori Valley, 11,500 ft., in the eastern Kumaon Hills, was obtained in fairly large numbers both from the Kulu and Spiti Valleys, at 11,000 ft. to 13,000 ft., from bare ground and from beneath stones and also from over snow at about 14,000 ft. on the Rohtang Pass. The species appears to be very hardy and was found alive on the snow. Both the species mentioned above have well developed wings and their geographical distribution lends support to the stenozonal nature of distribution of some of the high altitude insects. There are also a number of other species of the family in which the wings are either atrophied or are altogether wanting. Some of these belong to the genera *Stenus* and *Atheta* and were collected from localities between 11,000 ft. and 14,000 ft. Apterous species of Silphidae (*Silpha nitida* Port) and Meloidae (*Meloe* sp. near *servulus* Bates) were also collected from altitudes between 10,800—12,000 ft.

Several species of Tenebrionidae were also collected from beneath stones at different altitudes. *Platyscelis asidioides* Bates, was the commonest (over 150 examples collected) with *Platyscelis* sp. near *batesi* Kasz., as the next common species. The former, originally described from Kashmir, was collected from various localities in the Lahaul and Spiti Valleys, namely, Sissu (10,500 ft.) to Purana Khoksar (13,000 ft.), but none from any of the places in the Kulu Valley. The latter species was, however, obtained from Ralha (11,800 ft.) in the Kulu Valley but not from lower altitude. Both these species are apterous and of black colour. Species of *Blaps* and *Gonocephalum* also showed a similar altitudinal distribution.

Interesting material of Curculionidae was obtained from practically similar environments. Long series (over 100 examples of each) of *Blosyrodes pubescens* Marsh. and *Nephadonyoe ferus* Faust., were obtained from about 2 miles north of Ralha (1,000—12,000 ft.), near the source of river Beas and from Thaltu Thach (11,800 ft.), Ganddapu (11,000 ft.) and Chhatoru (11,000 ft.). Both these species are apterous and are previously recorded from Baluchistan & Kashmir (11,200 ft.), and the Pamirs respectively. Relatively smaller series of *Leptomias longulus* Faust., and *L. persimilis* Marsh., previously known from Simla and Kumaon Hills, and "North India" respectively were likewise collected from these altitudes as well as from the Rohtang Pass (*Ca.* 14,000 ft.) mainly under stones or from grassland. Again, both these species are wingless. *Catapionus basilicus* Boh., which is previously known from Central Asia, and Gilgit in Kashmir, and which has atrophied wings, was collected from Thaltu Thach (11,800—12,000 ft.) and the mountains above Ralha at 12,000 ft. About six other species, which yet remain to be determined, were also collected, and these also appear to conform to the general characters and pattern of distribution mentioned above. Almost all these species are black or piceous except perhaps the last one which has some green scales over the black body.

Majority of the Chrysomelidae collected came from lower altitudes, namely, Manali (6,000 ft.) and Katrain (*Ca.* 5,000 ft.), and were collected from plants. These belonged to various genera like *Coptocephala*, *Nodostoma*, *Chrysomela*, *Haltica*, *Merista*, *Hoplasoma*, *Galerucella*, *Macrima* and *Dactylispa*. Most of these are with light colouration or bright patterns. With the exception of *Haltica* none of these were found beyond 8,000 ft. Certain species of *Haltica* were obtained at Sissu (10,500 ft.) from cultivated willow (*Salix* sp.) as well as from over snow at the Rohtang Pass (*Ca.* 14,000 ft.) to which place these had apparently been blown. At Sissu, different varieties of *Nonarthra variabilis* Baly, were also collected from *Salix;* this species has previously been known from Jhelum Valley, Kumaon Hills. Two further species of Chrysomelidae that were obtained from higher altitudes were associated with grassland at dwarf vegetation and are small wingless and apparently undescribed species of *Crepidodera* and *Longitarsus*. The former was obtained from 12,000 ft. at 2 miles north of Ralha and is of black colour and the latter from this locality as well as the Rohtang Pass (*Ca.* 14,000 ft.), and is dark brown in colour.

Of the ladybird beetles (Coccinellidae) collected, the phytophagous species like *Epilachna ocellata* Redt., which is a pest of potatoes in the hills of northern India, was obtained at a maximum altitude of 8,000 ft., at Kothi, in the Kulu Valley and seems to be absent in the Lahaul and Spiti Valleys where cultivated fields are situated usually between 10,000 ft. to about 12,000 ft. Several other palaearctic and more widely distributed species were also collected. *Coccinella septempunctata* L., *Adonia variegata* (Goeze) and *Oenopia luteopustulata* Muls., not only extend to the eastern Himalayas but also to the plains of northern India. *Adalia tetraspilota* (Hope), previously known from Nepal and Afghanistan, was collected from Kothi (8,000 ft.) and *Lioadalia luteopicta* (Muls.), previously known from Nepal, northern China and Tibet, was obtained from Sissu (11,500 ft.) in the Lahaul Valley.

Several species of moths and butterflies were also collected at high altitudes. A noctuid moth, *Cteipolia acrophila* Hamps. (Fig. 4), proved to be of great interest. It was collected at altitudes between 11,800 ft. and 14,000 ft. at and near the Rohtang Pass. It rested in the crevices between grey stones and boulders with which it matched perfectly. A few examples were also obtained from the snow on the Pass. Its body which is about 13 mm. long, with a wing-expanse of 30 mm. is provided with dense woolly covering, and on the dorsal surface of the fore-wings, in addition to the usual scales, a fairly large number of uniformly distributed long hairs are present (Fig. 5). While the woolly covering of the body may be a means of protection against extreme cold, the use, if any, of the hair on the fore-wings is not properly understood. It was observed, however, that when small droplets of water from melting snow fell on the wings of the moth, these (droplets) at once rolled down leaving the moth as dry as ever. The result of this observation was confirmed experimentally by pouring droplets of water several times. Its proboscis is aborted, the fore-wings narrow and the body relatively bulky, especially in the female which contained some 300 eggs each. The moths were sluggish and seldom took to flight when disturbed. The eggs (dissected out from the abdomen) are rounded and of relatively large size. A vigorous search for these moths at lower altitudes proved fruitless, while at higher altitudes these were obtained without much difficulty. The species appears to be a true denizen of high altitude. The genus *Cteipolia* contains three species known from West Turkestan (*C. sacelli* staud.), Kashmir, Kardong, 1,400 ft. (*C. acrophila*), and Tien-Schen, China (*C. isotoma* Pung.). We shall refer to other Lepidoptera later with an account of other insects collected from snow at the Rohtang Pass.

Reference may briefly be made to the various ants, the colonies of which were generally observed under sheltered positions at the edges of rocks and beneath stones. Although the exact identification of the species is awaited, it appears that the distribution of species collected between 9,000 ft. and 13,000 ft. was greatly influenced by the altitude; certain species which were relatively scarce at lower altitude became more common as we went higher, while others disappeared altogether. In spite of the bitter cold at certain places ant larvae were present in certain nests.

A number of Hemiptera were collected from the meadows as well from sheltered situations near stones and rocks. The Homoptera, especially the aphids, will be referred to during the account of insect found on snow at the Rohtang Pass, but an apparently underscribed species of the Lygaeid genus *Aphanus* was collected from beneath the edges of stones in the vicinity of scanty and dwarf vegetation at the Rohtang Pass (*Ca.* 14,000 ft.). This is a small and nearly black species in which the hemelytra are distinctly shorter leaving the distal one-third of the abdomen uncovered and in which the wings are much reduced, like several species of beetles already mentioned.

INSECTS IN STREAMS AND RIVERS

A great variety of aquatic insects are met with at high altitudes in small pools and lakes, the slow to torrential streams and the fast flowing rivers, all of which usually contain ice-cold water. Almost all the orders of insects commonly known to have aquatic species are present. The Stone Flies (Plecoptera) were collected from Manali (6,000 ft.) to Chhatoru (*Ca.* 12,000 ft.) but with the exception of perhaps one or two species of *Nemoura*, which was collected from Kothi (8,000 ft.) in the Kulu Valley as well as from several places (including Chhatoru, as mentioned above) in the Lahaul and Spiti Valleys, most of these were not so widely distributed. Their nymphs were found in fair number in running water at many places but these did not occur gregariously. The adults of *Nemoura* sp. were seen, sometime in copula, commonly among stones on the bank of Chandra river.

The May Flies, Ephemeroptera, were present in greater variety as well as in numbers than the Stone Flies. The nymph of an undescribed species of *Baetis* were found living gregariously beneath stones under water at the bank of the river Chandra, at Khoksar (10,800 ft.), Dhorni Thach (11,800 ft.) and Chhatoru (11,800 ft.). The water would strike with great force against these stones and yet it was unable to dislodge the nymphs. When a stone was lifted out of water, however, scores of nymphs showed wriggling movement and fell into water only to swim back to the undersurfaces of other stones. Their subimagoes and occasionally the imagoes, were also seen in fair numbers among drier situations on the stones near the bank of the river. Nymphs of two species of *Leptophlebia*, an undescribed species of *Ephemerella*, as also an imago of another species of the latter genus, were obtained only from Manali (6,000 ft.), Kote (8,000 ft.) and Ralha (9,000 ft.) but not from higher altitudes. Nymphs of *Ecdyonurus* were, in addition, obtained from Ganddapu (11,000 ft.). Species of *Baetis* and of *Iron* were more widely distributed than those of the other genera, as these were collected from nearly all the stations visited. Adults of a species of *Epeorus* and nymphs of two species of *Ironopsis* were, however, obtained only from altitudes between 8,000 ft. and 11,000 ft. These genera belong to the north temperate regions and are generally holarctic, and occasionally nearctic. Most of these have been previously recorded from the north-western and eastern Himalayas, but only rarely (e.g. *Baetis*) from the other parts of India. The species, on the other hand, appear to be generally endemic, but with further collecting in the Himalayas these may prove to be more widely distributed than what is known at present.

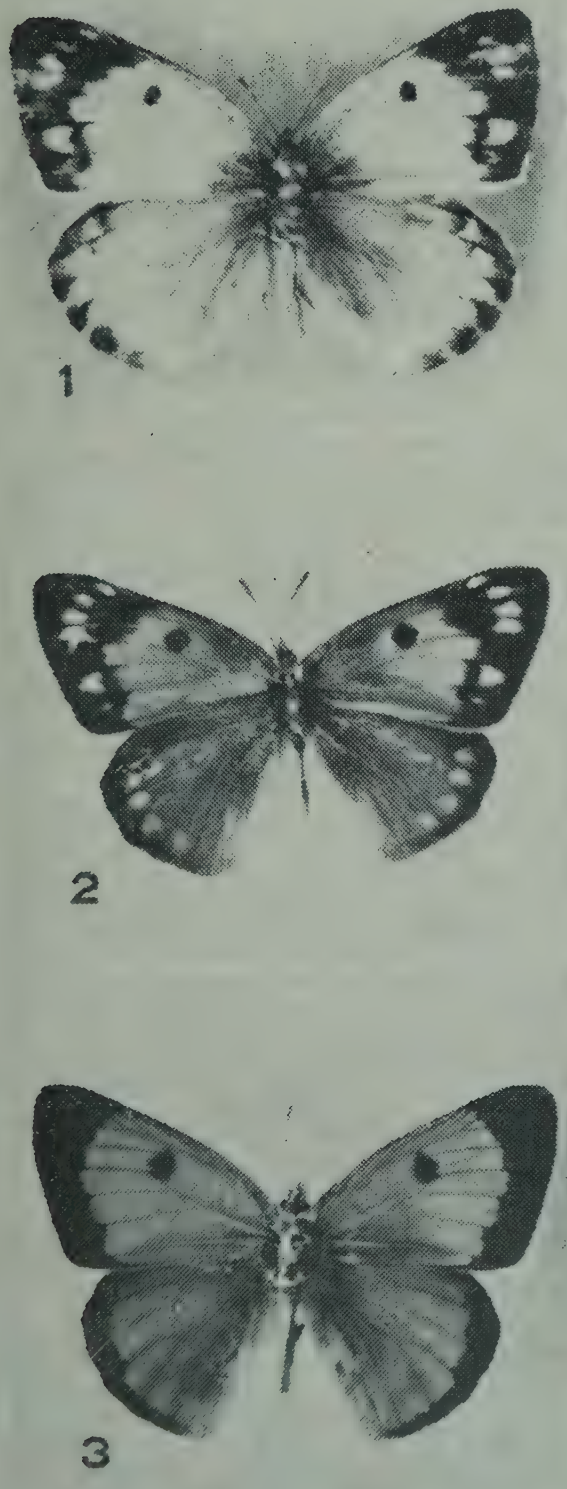
The Dragon Flies (Odonata) and the Caddis Flies (Trichoptera) were also present at the high altitudes, although perhaps in number of species the Trichoptera were richer than the Odonata. The larval cases of the Trichoptera were invariably made of different kinds of sand and gravel. Larvae of the large sized Limnephilidae, in cases made of coarse gravel and about 30-40 mm. long, were collected in shallow streams at Ralha (*Ca.* 9000 ft.), and Ganddapu (10,500 ft.). The species of smaller size, such as those of Rhyacophilidae and Sericostomatidae, were also collected at various elevations but since these have not been determined yet, much cannot be said about their distribution.

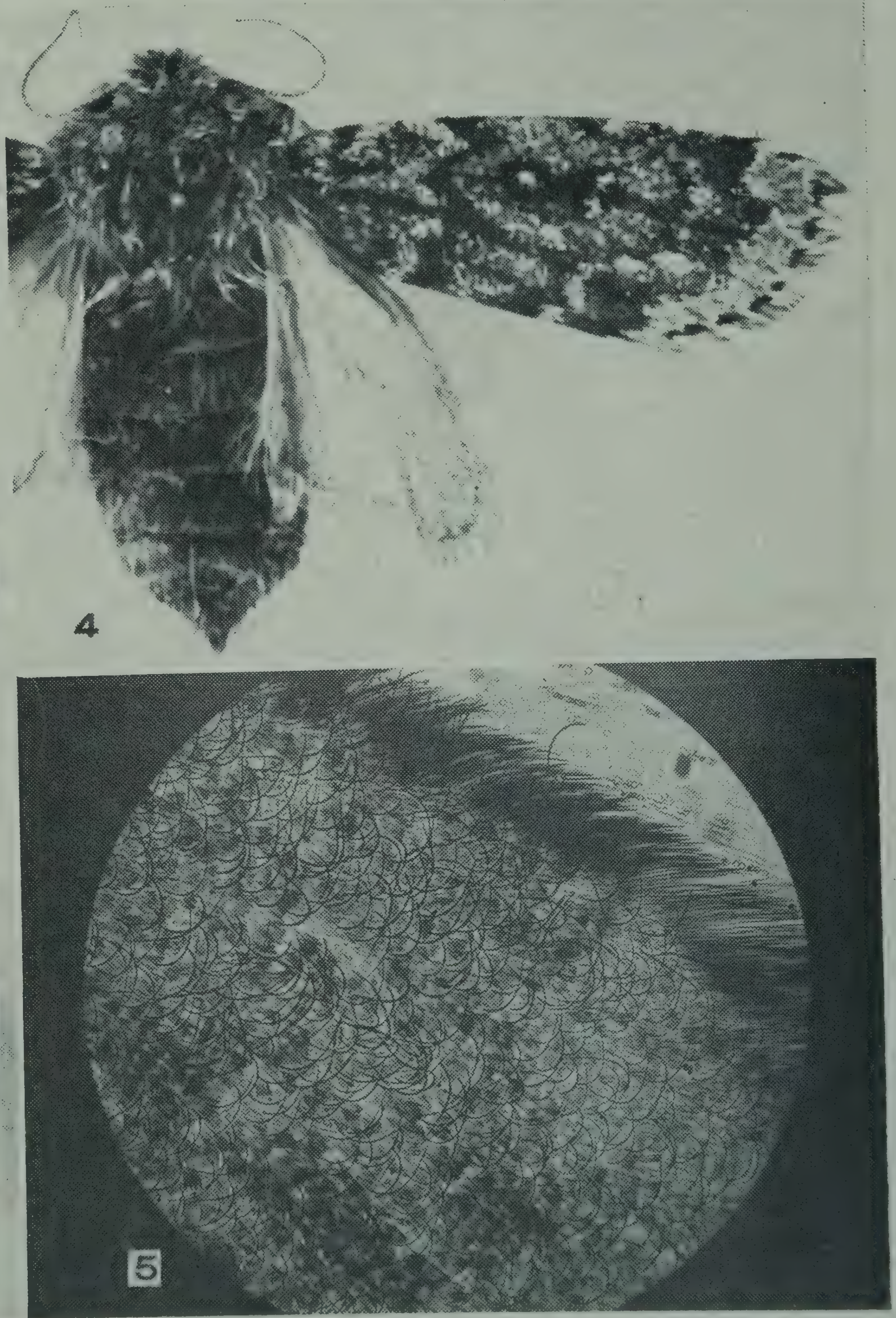
Of the aquatic beetles, a fair number of Hydrophilidae and Dytiscidae were collected at various altitudes. *Ametor rudesculptus* Sem., previously recorded only from Kashgar, Chinese Turkestan, was collected at Ralha (9,000 ft.) in the Kulu Valley. *Hydrocassis rugosis* Kirsch., *Regimbartia attenuata* (Tabr.) and species of *Laccobius*, *Helochares*, *Helophorus*, *Enochrus*, etc., were other Hydrophilidae found generally at 6,000 ft. The Dytiscidae were as a rule more common at higher altitudes than the Hydrophilidae. The commonest species of Dytiscidae collected was the well known palaearctic species, *Agabus* *biguttatus* (Olivier) from Manali (6,000 ft.) and Ralha (9,000 ft.) in the Kulu Valley and Ganddapu (11,000 ft.) in the Spiti Valley. It was found mostly in pools with algal slime and also in slow running water. It is black in colour. In the collections of the Zoological Survey of India this species is represented also from Simla, Kumaon and Mussoorie Hills which appear to be the eastern-most records of its distribution. *Rhantus pulverosus* Steph., *Bidessus geminus* (Fabr.) and *Canthydrus* sp., are among other Dytiscidae found at 6,000 ft. or so. Most of these are with bright colours or patterns. Several other species of the family from higher altitudes remain to be determined.

The aquatic, younger stages of Diptera were perhaps unsurpassed in number and variety by any other Order of insects associated with life in water. As it has not yet been possible to determine the material satisfactorily, nothing much may be mentioned except that these belonged generally to the Chironomidae, Culicidae, Simuliidae, Blepharoceridae, Tipulidae, etc. Sometimes the larvae of Simuliidae or Chironomidae were found gregariously on stones under water, in the slow running streams, generally at lower altitudes.

INSECTS ON THE SNOW COVERED ROHTANG PASS

With the mountains rising on either side to over 18,000 ft. or so, the Rohtang Pass (13,800—14,200 ft.) is the chief gateway to the Lahaul and Spiti Valleys from the Kulu





Figs. 1–3. *Colias electo fieldi* Ménétries (Pieridae). 1, white female form, *lucana* Rober. 2, orange female form. 3, male.

Figs. 4–5. *Cteipolia acrophila* Hamps. (Noctuidae). 4, female moth (X 4). 5, part of forewing greatly enlarged to show the long hair distributed among scales.

Valley. When covered with snow, and that condition lasts for most of the year except during a couple of midsummer months, the Pass is a virtual insect trap and offers excellent opportunities to the collectors. The strong winds from the north to south, and vice-versa, are a regular feature of the place and these no doubt obstruct the flight of many insects which, therefore, come to grief on the snow field at the Pass and the neighbouring mountains. There are also a number of other insects which are true denizens of the high altitudes and which subsist on dead or decomposed insects on the Pass. The apterous Carabid beetles of *Nebria* sp. were found on the hard snow at 14,000 ft.—14,200 ft. and so also certain collembola belonging to *Proisotoma* sp., at 15,000 ft. on the neighbouring mountain. This species was darker than other collembola collected. A large number of moths of *Agrotis ypsilon* Rott. which were found dead on the southern aspect but not on the northern aspect of the Pass were another source of food for certain dipterous flies which were sometime seen to fly away from the dead bodies of the moths. *A. ypsilon* is a well known pest of winter crops in the plains from where it is believed to migrate to the hills in the north during summer. It is possible that the moths were trapped at or blown over the snow at the Pass while these were migrating or flying for dispersal. The subject has been dealt with by me in greater detail in a separate paper (Kapur, 1956). The pierid butterflies, *Colias electo fieldi* Menetr. and *Pieris brassicae* Linn., are two other species that are known to migrate in these parts of India from the plains (Williams, 1930, pp. 38; 138). During the time of our visit also, these two species were observed to fly together in the northerly direction, although from their relatively fewer number than what has been recorded before, it must be presumed that we arrived there almost at the end of their migration period. The *Colias*, as is well known, show interesting polymorphism. Besides collecting the "orange" males and females, a few examples of the "white" female (form *lucana* Rober) of *C. electo fieldi* (Figs. 1–3) were also collected. Talbot (1939, p. 563) had stated that earlier record of *lucana* was due either to a wrong locality or to misidentification. Our catch, incidently, re-established the record of this form in India, from these parts of the Himalayas.

A number of other species of moths and butterflies were also collected at the Pass, either on wings or dead on snow. However, by far the larger number of species collected from snow belonged to the order Diptera. Some of these like *Phytomyza atricornis* Meig. (the pea leaf miner) and *Acanthiophilus helianthi* (Rossi) (the safflower fruit-fly) were found alive in quite large numbers on the snow. These species of the temperate region are well known pests in northern India but as these were found in quite large numbers for over a number of days at the Pass, it is probable that the sources from where these came were not far away from the Pass. *Hylemia cilicrura* (Rond.), *Hylemia cinerella* (Fln.) and *Oscinella frit* (Linn.), are among the other species which were also collected in fair numbers and which are also well known pests in several other parts of the world, especially in the palaearctic or holarctic regions. Majority of the Diptera collected from the Rohtang Pass belonged to the following families: Culicidae (*Anopheles gigas* var. *simlensis* James); Mycetophilidae (*Zygomia* sp.); Sciaridae (*Bradysia* sp.); Bibionidae (*Penthetria japonica* Wied. and *Bibio* sp.); Anisopodidae (*Anisopus* sp.); Chironomidae *Chironomus* sp., *Trichocladius* spp., *Diamesa* sp., and *Orthocladius* sp.); Dolichopodidae (1 species); Phoridae (*Megaselia* sp.); Tachinidae (*Macquartia* sp. and *Voria ruralis* Fln.); Calliphoridae (*Calliphora erythrocephala* Meig.); Muscidae (*Mydaea* (*Myiospila*) *meditabunda angustifrons* Mall., *Helina* (*Euspilaria*) *lucorum* Fln; *Coenosia* sp., *Schoenomyza litorella* Fln., *Pygophora* sp., *Lispe nana* Macq., *L. sericipalpis* Stein, *Hylemyia cilicrura* Rond., *H. flavibasis* Stein, and *H.* (*Paregle*) *cinerella* Fln.); Sciomyzidae (1 sp.); Lauxaniidae (*Pachycerina* sp.); Chamaemyiidae (*Leucopis puncticornis* Meig. and *Leucopis* sp.); Trypaneidae (*Acanthiophilus helianthi* Rossi); Otitidae (*Ulidia* sp.); Agromyzidae (*Phytomyza atricornis* Meig.); Borboridae (*Sphaerocera subsultans* L. and 3 species of *Leptocera*); Syrphidae (*Scaeva pyrastri* Linn. and *Epistrophe nectarinus* Wied.); Chloropidae (*Oscinella frit* Linn.) and Ephydridae (*Philygria flavipes* Fln. and *Scatella paludum* Meig.). The majority of these species are palaearctic or holarctic in distribution but a few belong to the oriental region also.

Of the Hemiptera, the Aphidae collected proved to be of considerable interest. *Cinara* (*Todolachnus*) *abieticola* (Chol.), *C.* (*Lachniella*) *comata* Doncaster, and two other species of the genus near *radicicola* Wellenstein, and *piceicola* Chol., were collected in fairly large number. The members of the genus *Cinara* are commonly known to infest conifers in different parts of the world, especially in the holarctic region. There is hardly any host-record of the genus from India. Only recently Doncaster has named the species, *C. comata*, from Nepal. The following conifers are found in these parts. Above the *chil* (*Pinus longifolia*) which extends up to 6,000 ft., occur the blue pine, (*Pinus excelsa*) and the *deodar*, (*Cedrus deodara*), together or severally. Between 8,000 ft. and 11,000 ft., the commoner species are the spruce, (*Picea moranda*) and the silver fir (*Abies pindrow*), the latter usually becoming pure at higher elevations.

Macrosiphum (*Sitobion*) *avenae* (F.), which is commonly known to infest ears of wheat in N. China, was also collected. Other species of aphids obtained from the snow on the Pass were *Cavariella aegopodii* (Scop.), *Eucarazzia elegans* (Ferrari), *Eriosoma* sp. near *ulmi* L. and *Lachnus* sp. near *pyri* Buckton. Here also, as in the case of most other collections that have been worked out, the genera are mostly palaearctic or holarctic but the species show a greater degree of endemicity.

GENERAL CONCLUSIONS

Although a lot more of insect collecting and field observations are required before my definite conclusions are arrived at about the nature of high altitude insects of these parts of the Himalayas, there is sufficient material available for drawing certain general conclusions, which may be briefly mentioned as follows:

1. *General reduction in the number of species.* In the parts surveyed in the Kulu, Lahaul and Spiti valleys, one observes a progressive reduction in the number of species of insects from about 8,000 ft. upwards. This is in keeping with the general diminishing of the vegetation and the increase in the severity of the climate, which is characterized by low temperature, humidity and atmospheric pressure. and high wind velocity and strong glare. The places at higher altitudes, even at 15,000 ft. or so, are, however, not devoid of life which seems to persist in various niches with favourable microclimate of their own. Although there is a general decrease in the number of species at such places, the number of individuals or populations of a species remain quite large. On this account it was possible to collect long series of many species.

2. *Greater association with soil or water.* The majority of the species living at high altitudes were cryptozoaic being associated with soil, especially in sheltered conditions near rocks or stones, or with water in glacial streams and rivers and the damp environments at their banks. Of the former a great majority were either carnivorous in habit or lived on dead and decomposed animal and vegetable matter. A large number of insects from neighbouring lower altitudes seem to reach these elevations either during the course of their normal process of dispersal or when carried high by strong winds. These appear to contribute substantially to the food supplies of the insect and other denizens of the high altitude. The moss, lichens and dwarf vegetation constitute other sources of food for the various forms including the high altitude weevils and chrysomelid beetles, etc.

On the other hand life in streams, rivers, pools and lakes was of a relatively greater variety and not always dominated by insects of predatory nature. Here also populations of individual species appeared to be considerable; the May Fly larvae of an undescribed species of *Baetis* in the Chandra River and larvae of certain Chironomids and Simulids, observed in great numbers are the cases in view. In general the aquatic forms were more adapted to life in rapid or torrential streams owing to the preponderance of the latter at high altitudes.

3. *Increase in pigmentation.* There is a general increase in pigmentation which is usually black, sometimes dark blue or dark brown. The collembolid species of *Proisotoma* collected from 14,000–15,000 ft. on snow was the darkest form of collembola that I had ever seen. The same is true of the Dermaptera and the beetles like the Carabidae, Staphylinidae, Silphidae, Meloidae, Tenebrionidae, Elateriade, Chrysomelidae and Curculionidae. Even the adults of aquatic Coleoptera belonging to Dytiscidae found at high altitudes were predominently black, while those of several other species from lower altitudes of 6,000 ft. or so, had a variety of pigmentation including the light colours. The same is generally true of many Diptera, Plecoptera, Lepidoptera, Hymenoptera (especially ants), Heteroptera (the Lygaeid, *Aphanus*, for instance), etc.

Much has been said about the increased pigmentation of species of insects from colder parts of the world and I believe the high altitude insects share this character with the former. It seems that the dark colouration helps them to absorb greater heat from the sun. It may be stated that Collembola, and other insects collected from ants' nests at high altitudes were white although the ants that had to go out foraging were of dark colour. The degree of dark colouration in the majority of aquatic insects that spend their immature and adult stages in quite different environments would appear to depend largely on the life span and habit of the species concerned.

4. *Reduction in wings.* As a general rule the apterous species of beetles specially certain Curculionidae, Carabidae, Staphylinidae, Silphidae, Meloidae and Chrysomeidae, etc., were found at high altitudes 10,000 ft. and above and seldom at lower elevations. In almost all cases such species were associated with terrestrial life. Species obtained from lower altitudes, even from beneath stones were invariably winged. The same was true of other species such as, *Aphanus* sp. (Lygaeidae), and the Curculionid, *Catapionus basilicus* Bol., in which the wings were considerably reduced. It appears that the apterous nature or the character of reduced wings are associated with the life at high altitudes. The prevalence of strong winds as a common feature at the high altitudes in these parts has already been mentioned. Under these conditions the apterous nature of species appears to be an asset.

5. *Increased hairiness.* Certain species of Lepidoptera such as the Snow Apollo butterflies (*Parnassius* spp.), which are well known denizens of the high altitudes, are characterised by increased woolly covering of the body. In the case of the Noctuid, *Cteipolia acrophila* Hamps., collected at high altitude, beside the prominent woolly covering of the body, the forewings are provided with a large number of long hairs. While the increased woolliness may be a protection against cold, the function of the hair on the wings is little understood, although it may possibly be a device to keep the moths dry.

6. *Geographical distribution.* From what is known of the fauna, it appears that the high altitude insects of these parts of the Himalayas belong predominently to the genera that are distributed in the palaearctic or holoarctic regions and only occasionally to the oriental genera. These genera are also extensively distributed in the Himalayas—including the eastern Himalayas. The distribution of the species is, however, not always as extensive, the majority of the species being endemic to the Himalayas and the neighbouring areas. A lot more collecting will have to be done in different parts of the Himalayas, in order to know the range of distribution of various species. From what is known of certain species belonging to a few groups such as the ground beetles and weevils that have been better worked out than others, it appears that the distribution of the species is quite extensive in different Himalayan ranges, as a number of them are known from as far east as Sikkim and seem to conform to a stenozonal pattern of distribution, which is facilitated by the generally transversely situated ranges.

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REFERENCES

Andrewes, H. E. 1924. Mission dans les Provinces Centrales de l'Inde et dans la région occidentale de l'Himalaya, 1914, par Guy Babault, Carabidae. 123 pp., 4 pl. Paris.

Andrewes, H. E. 1935. The fauna of British India, including Ceylon and Burma. Coleoptera, Carabidae, vol. 2, Harpalinae—I. xvi + 323 pp., 51 figs., 5 pls. London, *Taylor and Francis.*

Babault, G. 1922. Recherches zoologiques dans les Provinces Centrales de l'Inde et dans la région occidentale de l'Himalaya. 238 pp. Paris.

Burr, M. 1910. The fauna of British India, including Ceylon and Burma. Dermaptera. xviii + 217 pp., 16 figs., 10 pls. London, *Taylor and Francis.*

Hugel, C. F. von. 1840–48. Kaschmir und das Reich der Siek. vols. 1–4. Stuttgart, *Hallberger.*

Kapur, A. P. 1956. On moths of the greasy cutworm—*Agrotis ypsilon* Rott.—found dead in numbers on snow over Rohtang Pass, N. W. Himalayas. *Indian J. Ent.* 17 (3): 289–294.

Talbot, G. 1939. The fauna of British India, including Ceylon and Burma. Butterflies, vol. 1 (2nd ed.). xxix + 600 pp., 184 figs., 3 pl. London, *Taylor and Francis.*

Williams, C. B. 1930. The migration of butterflies. xi + 473 pp. Edinbrough, *Oliver and Boyd.*

The Insect Fauna of the Cape Verde Islands

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ABSTRACT

The greater part of the insect fauna of the Cape Verde Islands is Ethiopian and is spread chiefly over the steppe areas at lower levels. On the whole this fauna shows the same composition in all the islands of the archipelago. It consists for the greater part of smaller winged insects which have reached the Cape Verde Islands through wind dispersion. In the mountainous parts of the islands however an element of this fauna is to be found which seems to be of greater age—it consists of wingless specimens with a terricole way of life, or species confined to the lower shrubs and herbs. These species are endemic and mostly limited to a single island. There are also some genera which are endemic. The older element in the Cape Verde Islands is not macaronesian—it has nothing in common with the fauna of the Canary Islands. There has never existed any direct fauna-connection between the Canary Islands and the Cape Verde Islands, but both groups of islands have had connections with the eastern continent. The latest addition to the fauna of the Cape Verde Islands consists of species introduced by human agency, which in the Cape Verde Islands have had great opportunities of spreading.

Contrary to the other middle Atlantic or Macaronesian Islands the scientists have paid very little attention to the Cape Verde Islands. Between the years 1857 to 1860 the famous entomologist, V. Wollaston and his assistents visited these islands. They did not, however, reach all islands. In the year 1895 the Italian Zoologist Leonardo da Fea stayed a whole year on the Cape Verde Islands. In the year 1934 a French professor of Botany, Auguste Chevalier, collected some insects. In the year 1950 M. Cadenat from Dakar made a few collections of some insects. For 4 months during the winter of 1953–54 I made large collections of various insect groups on 13 of 15 islands in the Cape Verde archipelago. Later on the Spanish entomologist J. Mateu stayed for some time on the islands. There is very little published regarding many insect groups. Amongst the insects more attention seems to have been paid to the beetles than to any other groups. I also intend to talk mainly about the Coleoptera fauna.

Ten of the 15 Cape Verde Islands are a little bigger and inhabited, the rest small and rocky. The distance from the easternmost island to the African Continent is about 500 km, from the easternmost to the westernmost about 200 km, from the northernmost to the southernmost also 200 km. The predominant wind is the northeast trade wind, sometimes there is a hard desert wind blowing from the east. The western islands are volcanic, the eastern islands are very desert-like. The archipelago lies on about the 15th degree of northern latitude.

Wollaston notes (1867) in his Coleoptera Hesperidum 275 species from the Cape Verde Islands. He earlier visited Madeira and the Canary Islands and was an expert on the Coleoptera fauna of these islands. He was mislead by less essential similarities between the faunas and thought that the faunas of Madeira, the Canary Islands and of the Cape Verde Islands show near relationships to each other. A genus of beetles, which on the Canary Islands is very dominating and which there has produced a great number of species is the genus *Hegeter* of Tenebrionidae. One of the commonest species is *H. tristis*, found on the majority of the Canary Islands and on Madeira. The general occurrence of the wingless *H. tristis* on the Cape Verde Islands was according to Wollaston the most definite proof that the faunas of the Canary Islands and of the Cape Verde Islands were of common origin. Furthermore, Wollaston discovered on the Cape Verde Islands quite a lot of beetle species of various families similar to those he earlier had collected on the Canaries. This opinion of Wollaston regarding connection between the faunas of the Cape Verde Islands and the other Macaronesian Islands has been the basis of a later common opinion that the fauna of the Cape Verde Islands shows connection with the Mediterranean fauna, e.g. Holdhaus in "Handbuch der Entomologie".

If, on the basis of present knowledge about distribution, one makes a closer examination of the species which are supposed to represent a connection between the Cape Verde and Canary Islands, one may come to the following conclusion.

Firstly, the species Wollaston found on both groups of Islands either are common antropokores or species occurring on the African Continent in the transitional zone between the Palaearctic and Ethiopian regions. In Wollaston days knowledge about subtropic and tropic cosmopolites was very little, as was also knowledge of the continental African fauna. Regarding the peculiar species of *Hegeter* we can note the following. The genus *Hegeter* consists (except for *tristis*) of about 20 species, all of which occur only on the Canaries. Being tenebrionids without flying wings they have very small distributions, only one island or even only a part of it. Contrary to other *Hegeter* species, *tristis* has developed to an antropokore species which just as the *Blaps*-species, lives in cellars, storerooms, refuse heaps, and towns. As such a synantrope species it has been brought to Madeira and the Cape Verde Islands, where it has spread very much in the inhabited territories of the coastal zone. Thus one can say that the above-mentioned similarity between the faunas on the Cape Verde Islands and the Canary Islands essentially depends on the occurrence of antropokore species.

The dissimilarity between the faunas of the island groups is very prominent, especially if one takes into consideration the rich and very characteristic beetle fauna of the Canaries with its abundant endemic species and genera. Besides the above-mentioned tenebrionid genus *Hegeter* with some twenty species, the following among a great number of canarian endemics can be mentioned: *Carabus* with 4 species, *Calathus* with 20 species, the melolonthid genus *Ootoma*, *Pimelia*, the curculionid genera *Laparocerus* with about 75 species, *Lichenophagus*, and the group *Achalles*. The endemic species are nearly 40% of the 1300 species on the island group: the genera are palaearctic or of palaearctic type. None of the Canarian endemics exist on the Cape Verde Islands, that is: the two groups of islands have not a single beetle species, which does not exist elsewhere, in common. But Madeira and the Canary Islands have a few special species and genera, for instance the curculionid genus *Laparocerus*.

What are the characteristics of the fauna of the Cape Verde Islands? A coleopterologist who goes ashore on any one of the Cape Verde Islands very soon makes acquaintance with some species of the tenebrionid genus *Oxycara*. This genus corresponds exactly to *Hegeter* of the Canary Islands. Every island has at least one species, others two or three. Only very few species occur on two neighbouring islands. They occur in great numbers, some of them mostly in the lowlands, others mostly in the highlands. Wollaston distinguished 10 species, Dr. Gridelli, on the basis of Fea's material has made 6 new species, and my material contains another 2 new species. When one climbs higher up in the mountains one meets species of the tenebrionid genus *Trichopedus*, which, similarly to *Oxycara*, lives in colonies under stones. There are three species, or possibly races of one species, on each one of three western islands in the northern row of islands, and another well separated species on three western islands of the southern group. The three easternmost desert-like islands of the Cape Verde archipelago are each inhabited, especially on the upper parts of the volcano cones, by a species or race of the tenebrionid genus *Melanocoma*, like *Trichopedus* endemic to the archipelago. Under tussocks of psammophytes Wollaston found *Ammidium ciliatum*, a ballround tenebrionid. I found three new species of this endemic genus, each one on a different island.

The endemics living on the Cape Verde Islands occur especially in mountain territories, in the higher part of the cloud zone and in the zone above the clouds. Four islands have their own endemic species of the carabid genus *Cymindis*. Also peculiar is the curculionid genus *Dinas*, which corresponds to the canarian genus *Laparocerus*, though it is not so rich in species. These curculionids are mountain inhabitants, and can be found on low shrubs in the comparatively rich vegetation at higher levels. Each species occurs only on a single island, most of the islands having only one species. Wollaston discovered 5 species: I found 5 more species which have been described by the French specialist Roudier.

I could mention other endemic Coleoptera, but the endemics are not as numerous as on the Canary Islands. In my list of presently known Coleoptera of the Cape Verde Islands I have somewhat over 400 species: of these 80 are endemics; that is 20%.

Most of the beetle species on the Cape Verde Islands have a more or less wide distribution in the ethiopian region. We find these species in the vast desert and steppe zones of Sahara and Sudan. Some of them seem to be typical for Senegal and Nigeria, others also occur further north to eremic territories in the most southern part of the Palaearctic region in Egypt and Arabia. Regarding many of them, the most typical thing is that they, like numerous ethiopian species, can be found even in South Africa. The African element on the Cape Verde Islands mainly belongs to the steppe, sand, and saline territories, river ravines and cultivated ground. It dominates the vegetation fauna. I have estimated the part of the Coleoptera fauna which is formed by the African element to be 50%. It contains mainly small and middle sized species. The fauna contains only one cerambycid, a species common in Africa, and only one cetonid which is common in Africa.

It is quite clear that the percentage of African elements among other groups of insects is bigger. Thus we find among the Hemiptera a rich steppe fauna of African species. It is peculiar that the number of species of Hemiptera in the Cape Verde archipelago is nearly 250, nearly as great as the number of Coleoptera. It is not yet clear how high the percentage of endemic species of Hemiptera is. Also the fauna of Diptera contains mostly species with a vast spread in the ethiopian region. I want especially to mention a genus among the Flatids (Homoptera) which on the Cape Verde Islands is represented by a few endemic species. It is the genus *Cyphopterum* which in the Canary Islands has 14 species (all with a very restricted distribution), 2 species on Madeira, and one species on the Azores. In addition there are a few species in the western Mediterranean countries, and in the Atlas country. It is characteristic of these species that the flying wings are rudimentary and that they lack ability to fly. I have taken 6 species in the Cape Verde Islands; most of them were found in the mountain territories and are restricted to one island. The species living on the Cape Verde Islands form a separate group of species with strikingly common qualities in the morphology of the genital organs. Also a few Mirid genera show corresponding species in the mountain territories on the different Cape Verde Islands. My material of other insect groups is not yet worked out, so I cannot yet speak on the existance of endemic mountain forms among them.

As a summary of this report on the insect fauna of the Cape Verde Islands I might point out the following.

The greatest part of the fauna is African, it is above all distributed in steppe territories at lower levels. This fauna has on the whole the same composition on all islands of the archipelago. The African element contains mainly winged smaller insects, that by flight have been able to reach the Cape Verde Islands. The Coleoptera make a comparatively small part of the African element.

Mostly in the mountain territories, but also to some extent on lower levels there is a fauna element of apparently older date, it consists of wingless types with a terricole way of life or species confined to lower shrubs and herbs. These species are endemic and for the most part restricted to one island; a few genera are endemic. Only in regard to the dominating African element is it right to say that the fauna is very similar throughout the archipelago: as far as the older element is concerned the dissimilarity between the various islands is as great as between the different Canary Islands.

The older element on the Cape Verde Islands is not macaronesian and has nothing in common with the fauna of the Canary Islands: there has never existed any kind of faunal connection between the Canary and the Cape Verde Islands, but both the island groups have had connections with the continent to the east. The dissimilarity of the faunas indicates that these connections have been near one another neither in space nor in time. The *Cyphopterum*-leafhoppers are today spread over the rest of a part of northwestern Africa, which formerly stretched further out to sea. On the question of whether the fauna of the Cape Verde Islands is palaearctic or ethiopian, I would like to answer that the island group, being a boundary territory between two zoogeographical zones, has an older faunal element of more palaearctic type, a remainder from the time when the islands were connected with Africa, and a younger element which is pronouncedly ethiopian and which has spread to the islands since they were separated from Africa.

The latest addition to the fauna of the Cape Verde Islands consists of species introduced by human agency. As on many other islands these animals also on the Cape Verde Islands have had great opportunities of spreading. Owing to their inferiority the earlier species have not competed for space with the newcomers. The Cape Verde Islands should be a suitable territory for studies of the very interesting zoogeographical question, about the spread of the insects associated in different ways with human beings. The beetle species, which, in a wider sense, have been brought to the islands by human beings seem to make up about 30% of the total beetle fauna.

Le Peuplement entomologique de Madagascar

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RÉSUMÉ

Bien qu'encore assez mal connue, la faune entomologique de Madagascar a été l'objet, au cours des 10 dernières années, d'une somme très importante de découvertes et de travaux qui en ont complètement renouvelé l'image.

Plusieurs traits la caractérisent:

—une très grande richesse en espèce.

—un très haut degré d'endémisme, surtout spécifique, à un moindre degré générique, variant entre 75 et 100% selon les tribus.

—la présence de lacunes remarquables.

—la présence de formes archaiques dont les parents sont actuellement localisés en Afrique du Sud, Amérique du Sud et Australie.

—pour la très grande majorité des groupes d'Insectes les affinités sont strictement africaines.

—enfin dans de nombreuses familles on assiste à une extraordinaire diversification spécifique, plusieurs espèces pouvant être sympatriques.

Tous ses caractères semblent indiquer que le peuplement s'est fait, à partir de l'Afrique, par apports accidentels et évolution sur place.

L'évolution de la faune sur place s'est produite en partie par suite de la faible concurrence interspécifique, en partie à cause de l'extraordinaire diversité des habitats due au relief, à l'allongement Nord-Sud et à l'opposition des versants Est et Ouest.

Il n'est pas possible encore de distinguer des districts aussi tranchés que ceux que reconnaissent les botanistes. On est cependant tenté de distinguer: 1°—la côte Est, les parties encore boisées des plateaux et le Sambirano. 2°—les hauts sommets. 3°—le Sud, le Sud-Ouest et l'essentiel de l'Ouest.

Il existe peu de vicariants spécifiques dans ces trois régions, la différenciation étant aussi intense à l'intérieur de chacune d'elles qu'entre elles. Mais certains groupes ou genres sont localisés à l'une ou à l'autre d'entre elles.

Il y a un demi-siècle on considérait la faune malgache comme bien connue, et l'on croyait pouvoir en proposer une analyse biogéographique.

Depuis lors, les recherches d'entomologistes amateurs comme l'hyménoptériste Seyrig, le coléoptériste Vadon et le lépidoptériste Catala, ont si fortement enrichi l'entomofaune malgache que l'on pouvait douter du bien fondé de cette opinion. La création en 1947 de l'Institut de Recherche Scientifique de Madagascar a fait faire de nouveaux et considérables progrès à nos connaissances, par l'application des méthodes de récolte les plus modernes: piégeages à la lumière de Wood, lavages de terre, recherche des xénophiles et des nidicoles, élevages systématiques pour la recherche des parasites, et par la prospection de massifs isolés d'accès difficile. L'ampleur de ces progrès peut se mesurer à ce simple fait qu'en dix ans, plus de 2000 espèces nouvelles et une centaine de genres nouveaux ont été décrits de la Grande Ile; que cinq ordres et bien des familles qui n'avaient pas été signalés jusque là y ont été récoltés.

Mais l'importance même de ces découvertes, tout en modifiant profondément l'image que l'on se faisait de la faune malgache, conseillait la plus grande prudence dans l'interprétation des faits connus, que trop de nouvelles observations pouvaient démentir.

Il est cependant probable que, pour mal connue qu'elle soit encore, la faune entomologique malgache est aujourd'hui une des plus étudiée des faunes tropicales. Les remarques et suggestions qui suivent, basées sur l'état actuel de nos connaissances et sur neuf années de travail sur place, n'auront donc qu'une valeur d'approximation, mais d'une approximation que nous sommes en droit d'espérer assez satisfaisante.

Le premier trait remarquable de l'entomofaune malgache est le très inégal développement des divers groupes qui peuplent l'île.

Ainsi parmi les Coléoptères, quelques espèces malgaches de Scarabeini, Aphodiini, Onthophagini, alors que ces groupes sont très richement représentés en Afrique, s'opposent à une pullulation d'Hopliini et de Canthonini, rares en Afrique. Nous connaissons 6 *Onthophagus* malgaches contre plus de 1000 *Onthophagus* africains, mais une vingtaine d'*Aulonocnemis* malgaches et trente *Nycteropus* contre une espèce de chacun de ces genres en Afrique. Les Méloïdes, si diversifiés en Afrique, ne comptent que sept espèces malgaches.

Les Embioptères ne paraissent compter que trois espèces, largement pantropicales. Aucune forme endémique n'a encore pu être découverte.

Les Lycénides, les Nymphalides, les Acréides sont très mal représentés. En revanche, Satyrides et Hespériides se comptent par centaines d'espèces.

Et ces exemples pourraient être multipliés presque à l'infini.

Il n'y a donc aucun parallélisme entre le développement des divers groupes d'insectes des deux côtés du Canal de Mozambique. L'explication simple qui voudrait s'appuyer sur l'absence à Madagascar des milieux spéciaux favorables au développement de tel ou tel groupe ne peut être retenue, car la variété des climats malgaches, qui vont du subdésert à la forêt tropicale humide et du niveau de la mer à près de 3000 m. d'altitude, doit fournir des stations convenant aux espèces les plus exigeantes.

Un deuxième caractère de la faune malgache est l'extraordinaire pulvérisation en genres et surtout en espèces. Les genres comptant une centaine d'espèces malgaches, voir plus, ne sont pas rares. En biogéographie classique on serait tenté d'interpréter cette multiplication extraordinaire des espèces comme due à l'occupation, par des mutants, de toute une série de milieux légèrement différents et dans chacun desquels une espèce a pu s'isoler. L'analyse plus précise du phénomène ne permet pas de retenir cette interprétation. Un décimètre cube de terre peut fournir jusqu'à trois espèces du même genre de Bembidiides endogées, une branche d'arbre battue livre six ou sept espèces de *Neocolpodes*, le même excrément six ou sept espèces de *Sphaerocanthon*. Par une étonnante exception aux règles usuelles, les espèces affines et sympatriques sont très nombreuses; bien souvent aucune ségrégation géographique ou écologique ne paraît exister entre elles. L'emploi de la notion de double invasion ou de pénétrations successives ne rend pas davantage compte de cette coexistence; trop de formes, indiscutablement très affines et non moins indiscutablement bien distinctes, pouvant s'observer ensemble. L'emploi du concept de la superspecies de Mayr réduirait très sensiblement cette pulvérisation en formes sympatriques. Ainsi dans le cas des Anchomenini, 138 espèces malgaches sont énumérées par Jeannel (1951), et il faut leur ajouter six espèces décrites par le même auteur en 1956, d'un seul petit massif montagneux. Beaucoup de ces espèces comptent 4 à 5 sous-espèces. Or, 65 de ces espèces appartiennent au genre *Neocolpodes* et 51 sont des *Agonocolpodes*. Chacun de ces genres se divise en sous-genres: 6 pour *Neocolpodes* et 4 pour *Agonocolpodes*. Parmi les *Neocolpodes*, les sous-genres *Opisthopiesis* et *Acidotelus* se divisent à leur tour en deux "groupes d'espèces", le sous-genre *Neocolpodes sensu stricto* en cinq groupes. Parmi les *Agonocolpodes* les sous-genres *Piezotelus* et *Apocolpodes* comptent quatre groupes d'espèces chacun et le sous genre *Ectobothrus* en comprend trois. A examiner de près les groupes ainsi définis, on ne peut s'empêcher, tout en reconnaissant l'individualité des formes qui les composent, de les trouver si étroitement affines que le groupe d'espèces prend le caractère d'une véritable entité systématique. En considérant que, dans les cas de variation intense, la superspecies a la valeur d'une espèce classique dans les groupes où la variation est faible, on obtiendrait un tableau de la faune malgache nettement moins aberrant, où l'intensité de la spéciation serait réduite dans les groupes diversifiés et inchangée dans les autres.

Malgré tout, que l'on retienne la notion des superspecies ou qu'on la rejette, l'extraordinaire variabilité des formes malgaches mérite d'être soulignée. Précisons à nouveau qu'elle n'atteint pas tous les groupes. Bernardi remarque son absence chez les Piérides, et les dernières études de Jeannel ne la retrouvent pas—peut-être faute de matériel suffisant—chez les Psélaphides. Nous avons signalé plus haut son absence dans d'autres groupes. Notons en passant que lorsque, à Madagascar, les espèces d'un groupe sont largement eurytopes, ce groupe ne montre pas de spéciation intense mais que, bien souvent sympatriques, les espèces des genres très diversifiés sont toujours étroitement localisées.

On pourrait être tenté d'invoquer la notion de spéciation explosive de Woltereck, (qui se retrouve dans l'effet instantané de la dispersion en éventail du P. Teilhard de

Chardin) mais en se pénétrant de l'idée que l'évolution des espèces malgaches a été très rapide. Nous n'avons que peu d'exemples certains de cette rapidité d'évolution qu'il faut rapprocher du principe de Mayr "evolution should proceed more rapidly in small populations than in large ones". Cependant un de ces exemples vaut d'être cité. Alors que la faune africaine renferme un certain nombre de Tenthrèdes, et en particulier des espèces d'*Athalia*, la faune malgache ne possède qu'une seule Tenthrède (en laissant de côté une sous-famille spéciale de Cephidae), *Athalia malagassa* Sauss. Or cette espèce vit sur les Crucifères cultivées introduites (les Crucifères sont infiniment rares à Madagascar en dehors des espèces cultivées: Radis, Chou) et sa biologie comme sa morphologie sont étroitement proches de celles d'*A. colibri*, espèce holarctique acclimatée en Afrique du Sud. Détails de la ponte, biologie des larves, tout rappelle cette dernière espèce. Il est impossible dans ces conditions, de ne pas penser qu'*A. malagassa* est un vicariant local développé à partir d'*A. colibri*. Mais, vivant sur des Crucifères importées d'Europe (et semble-t-il localisée aux Plateaux), *A. malagassa* n'a pu être introduite qu'au cours du XVIIe siècle au plus tôt. Ce très bref laps de temps, trois siècles au plus, a pourtant permis la formation d'une espèce individualisée.

L'étude des couples vicariants qui s'observent dans les lambeaux de forêts qui subsistent encore sur les plateaux, parle dans le même sens. Au XVIIIe siècle le couvert forestier des plateaux était, au dire des voyageurs, largement continu; l'isolement, plus récent, de massifs isolés, a permis la formation de vicariants caractérisés et ces vicariants se retrouvent dans toute une série de groupes: Ptérostichines, Brachynes, Dryptines des Carabiques, Osoriens, *Paederus* des Staphylins, Coptomia des Cétonides, Curculionides, Satyrides, Tipulides, *Ravenalites* et *Uranotaenia* des Culicides, *Nesolestes*, *Protolestes*, *Pseudagrion* des Zygoptères. Il est ainsi possible de dresser, pour le moindre lambeau forestier une liste d'endémiques qui comprend facilement une cinquantaine d'espèces que l'on ne retrouvera pas dans le massif voisin, à 50km. de là.

En dehors de l'intérêt théorique de cette constatation, une considération s'impose si l'on veut réaliser quelque jour un inventaire valable de la faune malgache.

Tout nous porte à considérer que la faune entomologique malgache actuelle est en pleine évolution et que cette évolution est très rapide.

A cette spéciation poussée correspond un très haut degré d'endémisme, surtout spécifique mais non négligeable parmi les genres. Cet endémisme spécifique varie entre 75 et 100% dans la plupart des groupes; il ne descend, exceptionnellement, à 50% que dans certains groupes connus pour leur vaste distribution (Coccides par exemple) et n'atteint des taux inférieurs que pour les Aphides où seules des espèces anthropophiles sont connues. La récente découverte de deux espèces endémiques d'Aphides actuellement en cours d'étude par le Professeur Essig, montre cependant que cette situation n'est sans doute que temporaire. Un endémisme aussi élevé allié à une faune riche est véritablement exceptionnel; l'endémisme en particulier est nettement plus faible dans les îles voisines comme les Mascareignes et la faune est proportionnellement moins riche en Australie ou en Nouvelle-Zélande.

Il convient cependant de souligner que s'il existe des familles botaniques endémiques de Madagascar, aucune famille d'Insectes et sans doute (le cas des Cétoines malgaches doit être réservé jusqu'à plus ample étude; celui des *Hexodon*—dont les seuls parents reconnus appartiennent à un genre néocalédonien d'affinités en réalité incertaines—serait plus valable) aucune sous-famille n'est propre à la Grande Ile. L'ampleur du mégaendémisme ne s'accompagne pas d'un endémisme à l'échelon de la famille ou de la sous-famille. Ceci doit, peut-être, s'interpréter comme dû à une très faible concurrence vitale qui, tout en ne limitant pas une spéciation explosive, n'impose aucune évolution et permet aux groupes archaïques de conserver leurs traits originels.

Pour riche et spéciale qu'elle soit, la faune entomologique malgache, comparée à la faune africaine, présente de surprenantes lacunes, lacunes qui se constatent parmi les groupes les plus largement répandus comme les plus spécialement éthiopiens. Dans l'état actuel des recherches manquent ainsi les Membracides, les *Chlorolestes* des Odonates, les Termites africains primitifs (*Hodotermes*, *Stolotermes*, *Porotermes*, *Microhodotermes*, *Anoplotermes*), de nombreux groupes de Coléoptères: *Gymnopleurus*, *Sisyphus*, *Copris*, *Catharsius*, pratiquement tous les groupes africains et indoafricains de Cétonides, de nombreux groupes de Nymphalides, pour ne citer que les plus évidentes de ces absences.

Si l'on analyse la faune connue quant à ses origines, on peut y reconnaître, en dehors des formes pantropicales:

1)—un élément austral, peu important numériquement, mais qui a une valeur théorique considérable: Cicindélides arboricoles à affinités sudaméricaines, *Pauliamma* des Blépharocérides Edwardsininae, *Campodella* des Campodéides, Plécoptères. Parmi les paléoendémiques peu étudiés, par exemple parmi les Curculionides, d'autres seront certainement découverts si l'on en juge par de récentes découvertes à la Réunion, et par la présence à Madagascar d'un genre de la sous-famille américaine des Cholinae: *Homalomorphus* Hust. Il s'agit de formes qui, typiquement (Blépharocérides), se retrouvent au Sud de l'Amérique du Sud, en Australie ou Tasmanie et en Afrique du Sud. Fréquemment ces groupes manquent dans une ou plusieurs de ces masses territoriales, mais elles ont toujours, avec une répartition australe plus ou moins incomplète, le caractère de formes archaïques.

Le caractère fragmentaire ancien de ces représentants austraux ne permet de les interpréter que comme les descendants de formes qui ont émigré du Nord vers le Sud et n'ont survécu que dans des asiles où les formes plus progressives, actuellement à dominance holarctique, n'ont pu pénétrer.

2)—un élément éthiopien. C'est, et de très loin, l'élément le plus important, aussi bien par le nombre que par la variété des groupes en cause. Plus de 80% de la faune malgache est à affinités éthiopiennes étroites et cette proportion serait la même, que l'on base les calculs sur les superspecies, les espèces ou les genres.

La répartition de la faune entomologique de l'Afrique Continentale est encore trop mal connue pour que la faune de Madagascar puisse être rattachée plus spécialement à celle de telle ou telle région africaine. Cependant de particulières affinités se dessinent avec la faune de la province du Cap et des régions semi-désertiques du Sud-Ouest africain. Comme il fallait s'y attendre, ces affinités portent principalement sur les éléments habitant le Sud et le Sud-Ouest, sub-désertiques, de la Grande Ile. Citons les Hopliini et en particulier les formes à fémurs postérieurs hypertrophiés, le *Neomnematium* aptère, les Tentyriides que le Dr Koch vient de découvrir.

Leur semblable localisation en zone semi-aride en Afrique et à Madagascar, ne paraît pas, le plus souvent, tenir à un quelconque refoulement centrifuge par des formes plus jeunes, mais à des besoins écologiques précis et comparables.

Mais certains de ces éléments éthiopiens ont le caractère de reliques très caractérisées: citons le genre *Brachynillus*, avec une espèce cavernicole et aveugle du Tanganyika et une espèce microphtalme et orophile du Sud de Madagascar; les Osoriens endogées localisés apparemment à certains massifs centre-africains, mais très largement distribués à Madagascar dans les zones Centre, Est et du Sambirano; les Ténébrionides endogées localisés à certaines stations favorisées de l'Ouest africain et très répandus à Madagascar (dans ce dernier cas on pourrait aussi penser à des formes australes car des genres voisins se retrouvent en Nouvelle-Zélande).

Il est encore trop tôt pour dater les arrivées de représentants africains à Madagascar. On peut cependant y reconnaître:

a)—une couche ancienne, qui a donné naissance à des genres endémiques, formée d'espèces surtout terricoles, souvent aptères, dont on peut supposer que la pénétration s'est faite lorsque Madagascar était relié à l'Afrique, donc au Crétacé au plus tard.

b)—des couches plus récentes, pour lesquelles on n'observe qu'un microendémisme ou un mésoendémisme; l'arrivée de ces formes se situe depuis la séparation, elle est assez ancienne pour que les espèces aient pu occuper toute l'île ou du moins d'importantes surfaces, mais avec des densités très variables.

c)—des arrivées récentes, subactuelles ou actuelles, dont les représentants n'ont pas changé depuis leur arrivée, et dont les plus récentes n'ont pas étendu leur aire de distribution au-delà de leur point d'arrivée.

Un très bon exemple de ces diverses répartitions nous est donné par le complexe *Helictopleurus-Onthophagus*.

Les *Helictopleurus* constituent un genre endémique riche d'une trentaine d'espèces, extraordinairement diversifié dans sa morphologie et qui, éthologiquement comme morphologiquement, répond aux *Diastellopalpus*, *Oniticellus*, *Euoniticellus* et à une partie des

Onthophagus africains. Parmi les nombreuses espèces, la majorité est assez étroitement localisée et la spéciation encore actuelle est évidente. Il s'agit là de paléoendémiques très caractérisés qui, parfaitement en place, colonisent, par des formes vicariantes, les divers biotopes.

Les *Onthophagus* comprennent cinq espèces:

O. pipitzi Ancey, *O. hinnulus* Klug, *O. elegans* Klug, espèces endémiques, assez largement distribuées dans l'île, mais rares et localisées, n'ayant pas encore manifesté de tendances à la spéciation, affines à des espèces africaines.

O. catta F., espèce indo-africaine à vaste distribution, parfaitement eurytope.

O. depressus Har., espèce africaine découverte il y a quelques années (1953) dans la région de Tuléar et localisée à environ 100 km. de côte, au Sud et au Nord de cette ville, de Manombo à Anakao.

3)—un élément oriental. Celui-ci apparaît chez les Diptères, certains Orthoptéroïdes, certains Histérides, certains Rhopalocères. Il est toujours très peu important numériquement et affecte spécialement les formes de la forêt tropicale humide. Dans de nombreux cas, cet élément oriental peut avoir été importé par l'homme (*Sipyloidea sipylus* Westw.) ou être venu à Madagascar par voie de migrations actives (certains Anisoptères), ou passives (*Corethrella inepta* Ann.); pour d'autres, *Phlebotomus squamipleuris* Newst., la présence non seulement à Madagascar mais en Afrique Orientale ou à Zanzibar ne permet pas d'exclure soit un transport par l'homme, soit une migration avec relais africain, et de choisir entre les deux hypothèses. Il est très important de rappeler ici les observations de Lesne qui soulignait le parallélisme entre la distribution des Bostrychides et les courants migratoires et commerciaux des hommes.

Enfin, quelques éléments ne paraissent relever d'aucune de ces explications et appartenir réellement à un fonds oriental. La localisation de cet élément dans la zone orientale, le fait qu'il s'agit surtout de formes xylophages (tel un Niponiidae), que les îles situées plus à l'Est de Madagascar (Tromelin, Maurice, la Réunion) ont des éléments orientaux plus nombreux que ceux présents à Madagascar, et qu'il s'agit d'îles océaniques, permet de penser que ces éléments asiatiques sont parvenus à Madagascar uniquement par voie de transports passifs en utilisant les vents et les courants dominants.

4)—A. Seyrig soulignait la présence d'un élément boréal représenté surtout en altitude et parmi les petites formes ailées d'Hyménoptères. Le développement à Madagascar et aux Mascareignes de certains groupes boréaux, faiblement représentés en région tropicale, tels les Coniopterygidae est à en rapprocher.

L'interprétation la plus satisfaisante est que ces formes, à large pouvoir de dispersion par les courants aériens, n'ont pu se maintenir en présence de la faune tropicale classique dans les nombreuses stations où elles ont pris pied, que dans des biotopes où cette faune n'apparaissait que filtrée. Et l'on pense au rôle destructeur que Dahl prêtait, il y a près de cinquante ans, aux Fourmis, en zone tropicale.

Dans un essai publié en 1952, nous soulignions que le peuplement de Madagascar évoquait celui d'une gigantesque place vide. La même année, puis dans des publications ultérieures, J. Millot, étudiant le peuplement global de Madagascar et insistant plus spécialement sur le cas des Mammifères, concluait à un isolement total et très ancien de Madagascar qui n'aurait reçu, depuis, des éléments de sa faune que par apports passifs ou migrations aériennes. L'analyse des récoltes faites par J. Millot et les collaborateurs de l'I.R.S.M. aux Comores, par Viette et nous-même à la Réunion, par nous à Europa et Tromelin, soulignent aujourd'hui la vraisemblance de cette thèse. Elle montre en effet que la région malgache[1] est formée d'une série de blocs insulaires indépendants et hétérogènes et établit que chacun d'eux constitue la limite de pénétration vers Madagascar de formes asiatiques ou africaines: *Protaetia* aux Mascareignes, *Mausoleopsis* aux Comores et à Europa par exemple.

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[1] Le terme est pris ici uniquement au sens géographique; il vaudrait mieux dire la *région insulaire de l'Océan Indien Occidental*, ou peut-être la *Macronésie Indienne*.

Madagascar constitue ainsi, à l'échelle d'un petit continent avec ses climats diversifiés et ses milieux si variés, une gigantesque expérience naturelle permettant d'étudier les conditions d'implantation et ses conséquences, dans un milieu à l'origine presque azoique. Peu de régions du globe présentent un intérêt comparable pour l'étude de la formation des espèces. Il serait à souhaiter que des concours suffisants soient apportés à l'oeuvre entreprise par l'Institut de Recherche Scientifique de Madagascar pour lui permettre de la mener à bien et qu'un effort international porte sur l'inventaire et l'écologie de l'entomofaune malgache.

L'Entomofaune de l'Ile de la Réunion

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RÉSUMÉ

La Réunion ou Bourbon, située à 800 kilomètres à l'est de Madagascar et à 200 kilomètres au sud-ouest de Maurice, est entièrement volcanique. Elle est constituée de deux volcans accolés, l'un éteint au nord-ouest (le Piton des Neiges, 3.069m) l'autre actif au sud-est (le Piton de la Fournaise, + 2.500 m).

Température chaude dans la ceinture des plaines côtières (culture de la canne) de plus en plus fraîche dans l'intérieur, suivant l'altitude.

Végétation primitive comprenant cinq types principaux. La forêt très hygrophile, entre 1.000 et 1.800 m dans les régions pluvieuses de la partie du vent est la mieux conservée.

Un travail d'ensemble sur l'entomofaune de l'île a été fait dans le Livre de Maillard (1863). Depuis quelques travaux, grâce aux récoltes de Sikora, Alluaud, Bordage, Carié, J. Vinson, Hamon ont été publiés. Une mission franco-mauritienne y fit récemment un séjour.

La faune est pauvre. On notera le grand développement de certaines familles: Lyonetiidae Metachandidae, Curculionidae, l'île ayant probablement, à un certain moment, fonctionnée comme place vide. A part quelques exceptions typiquement indo-australiennes, la presque totalité de la faune est mauritienne, malgache ou éthiopienne, avec de nombreuses espèces paléotropicales.

A un moment où la question de la biogéographie de Madagascar, grâce à l'étude de l'abondant matériel récolté pendant ces dix dernières années par l'Institut de Recherches scientifiques et ses collaborateurs, se présente sous un jour nouveau (non classique, mais certainement plus exact), il était intéressant de connaître également la faune de l'île de la Réunion, la plus proche des Mascareignes, mais aussi la plus mal connue. Une mission franco-mauritienne put, en janvier-février 1955, récolter dans différentes régions de l'île et notamment en altitude. Vu la pauvreté relative de la faune, les collections furent importantes et le résultat de leur étude a déjà été publié dans un des volumes des Mémoires de l'Institute scientifique de Madagascar (sér. E, vol. 8, 1957).

La Réunion ou Bourbon, la plus occidentale des trois îles de l'archipel des Mascareignes, est située à 780 km à l'est de Madagascar, à la hauteur de Mananjary, et à 195 km au sud-ouest de Maurice. Ayant, en gros, la forme d'un cercle un peu aplati, l'île, dans sa plus grande longueur, ne dépasse pas 70 km et 50 dans sa plus grande largeur. Son pourtour est de 213 km et sa superficie de 2.512 km^2.

Entièrement volcanique, cette magnifique île est constituée de deux volcans accolés, l'un éteint dépassant 3.000 m, vers le nord-ouest, le piton des Neiges et l'autre en activité atteignant presque la même altitude, vers le sud-est, le piton de la Fournaise. Le massif du piton des Neiges est formé d'un vaste ensemble composé des trois cirques de Salazie, Cilaos et Mafatte. Les saisons sont bien marquées et au nombre de deux: la saison sèche pendant l'hiver austral et la saison des pluies pendant l'été. Le relief et les vents partagent l'île en deux régions: l'une à axe dirigé vers le nord-est, la région au vent et la plus arrosée, l'autre à axe dirigé vers le sud-ouest, abritée, la région sous le vent. Sur la côte, le maximum de la température est de 32° et le minimum de 15°. L'intérieur peut être très froid avec de la gelée blanche. Les pluies augmentent avec l'altitude: 990 mm à Saint-Denis, sur la côte nord, 2.184 mm à la Plaine des Cafres à 1.530 m d'altitudes Cependant certaines moyennes sont faussées par les véritables déluges cycloniques. C'est ainsi que dans la seule journée du 23 décembre 1934, à la Plaine des Palmistes (1.100 m), il est tombé plus de 1,10 m. d'eau et le pluviomètre fut observé trois fois débordant; en février 1949, il tomba à Takamaka (900 m) 3.513 m d'eau en 12 jours, presque autant qu'à Tamatave en un an. De plus, il faut souligner l'importance des précipitations occultes dans la forêt d'altitude (cloud forest) provenant de la condensation des nuages sur les feuilles.

Contrairement à la faune, la flore est fort riche, mais c'est là un cas assez général pour beaucoup d'îles volcaniques récentes. La végétation primitive comprend, d'après Rivals, cinq types principaux:

1°° une ceinture maritime très restreinte.

2°° un territoire mégathermique sec, restreint dans les régions inférieures chaudes et arides de la partie sous le vent.

3°° une ceinture de forêts complexes que l'on peut diviser en forêt de basse (presque entièrement détruite), moyenne (en partie détruite) et haute altitude.

4°° la forêt de Tamarins des Hauts (*Acacia heterophylla*) et de Calumets (*Nastus borbonicus*) située entre 1.200 et 2.000 m, limitée aux régions abritées de l'alizé.

5°° les étendues des hautes altitudes au dessus de 1.800 2.000 m couverte d'une végétation éricoïde à *Philippia* (principalement *Ph. montana*) et *Helychrysum*.

La végétation de la plaine côtière, et jusqu'en moyenne altitude, a été détruite pour faire place à la culture de la canne à sucre, avec, au dessus, celle des plantes à parfum.

Il est à peu près impossible de dire quand les premiers Insectes réunionnais arrivèrent en Europe; certainement, déjà au XVIII° siècle on connaissait quelques Insectes spectaculaires de Bourbon puisque le *Papilio* endémique: *P. phorbanta* est décrit par Linné en 1771 mais avec une indication erronée "*habitat in Cayenna.*" Il est fort probable que, dans les premières années du XIX° siècle, des Naturalistes, comme Bory de Saint Vincent, aient récolté des Insectes, mais il n'existe aucune trace de ce matériel. Il faut attendre les années 1830 pour avoir des renseignements précis avec les collections de Bréon, Goudot, Poutier et Sganzin. Comme Entomologistes ayant travaillé à la Réunion il faut citer Ch. Coquerel qui y fit 3 séjours et y mourut. Ses travaux et ceux de Fairmaire sur les Coléoptères de l'île sont classiques. Auguste Vinson, né et mort à la Réunion, esprit cultivé, auteur de plusieurs ouvrages scientifiques et littéraires. Maillard, auteur d'un livre classique, "Notes sur l'île de la Réunion". Ch. Alluaud qui y fit deux séjours. Ed. Bordage, connu par ses travaux sur l'autotomie et la régénération des Phasmides, s'intéressa aux parasites de quelques plantes d'importance économique. P. Cariée, industriel mauritien, y séjourna en 1898 et 1921. Enfin pour finir, il faut citer les noms de Jean Vinson et de J. Hamon.

A quelques exceptions indo-australiennes près, la faune est éthiopienne et malgache, avec dans certains groupes de nombreux genres et espèces paléotropicaux. Sur 120 espèces de Lépidoptères bien connues systématiquement (les autres espèces n'ont pas été retenues), 58 (principalement des Pyrales) sont répandues dans toutes les zones chaudes du Vieux Monde, 32 se trouvent à la fois en Afrique, à Madagascar et dans les Mascareignes, 11 sont uniquement malgaches, 4 se retrouvent à la Réunion et à Maurice et 14 représentent une espèce ou une sous-espèce endémique. Celles-ci sont rattachables à des groupes africano-malgaches, le Danaïde *Euploea goudotii* étant seul typiquement oriental. De nombreuses familles sont absentes (Saturniidae, Notodontidae, Lasiocampidae p. ex.) ou peu représentées (Arctiidae, p. ex.). Par contre, les Sphingidae, bons voiliers, sont assez nombreux, presque toutes les espèces malgaches s'y trouvant. Deux familles de Tineoidea, s.l. (les Metachandidae et les Lyonetiidae) se sont pulvérisées en un grand nombre d'espèces alors que peu de familles de ce groupement sont présentes.

La faune des Carabiques montrent que les Mascareignes font intimement partie de la région malgache. La Réunion et Maurice ont une faune autochtone formée de nombreux éléments africains et d'un petit nombre d'éléments indo-malais, dans la même proportion qu'à Madagascar (R. Jeannel, 1953, Le Natur. malg., 5, p. 61).

Un grand Staphylinide, typiquement cavernicole, a été trouvé, avec sa larve, dans une caverne de la plaine des Cafres. A noter que c'est, peut-être, le premier Coléoptère cavernicole vrai trouvé dans une grotte établie en terrain éruptif, car il était jusqu'ici admis que les cavernicoles ne se trouvaient seulement que dans les terrains calcaires. L'espèce appartient à un genre répandu dans les régions paléotropicales et est très voisine d'espèces vivant à la surface. Il s'agit sans aucun doute d'une espèce venant de l'extérieur et s'étant adaptée à la vie cavernicole.

Les Curculionides, comme dans beaucoup d'autres faunes insulaires (les îles de la Polynésie, p. ex.) ont atteint un très grand développement avec de nombreuses espèces nouvelles.

De même que les Lépidoptères, les Orthoptéroïdes, à quelques exceptions orientales près, sont africano-malgaches, avec beaucoup d'espèces endémiques voisines d'espèces africaines et surtout malgaches.

La plupart des autres ordres d'Insectes sont trop mal connus systématiquement (comme les Hyménoptères ou les Diptères), peu représentés à Bourbon ou même absents, pour pouvoir en tirer quelques données biogéographiques. De plus leur connaissance est également insuffisante dans les régions voisines.

En conclusion des quelques faits exposés ci-dessus, il est facile de dire que la faune de la Réunion est avant tout une faune d'origine africo-malgache, avec seulement quelques éléments indo-australiens. Quand à l'origine de cette faune, je me garderai bien de prendre position. Je dirai seulement que, quelque soit la théorie à laquelle on fasse appel, la pauvreté de la faune s'explique facilement. Par suite de la forme actuelle du relief, l'ampleur des éruptions volcaniques a dû être considérable et détruire une grande partie de la faune primitive, ou, l'île étant d'origine récente (plus récente que Maurice) les transports passifs n'ont pas encore permis à l'île d'avoir une faune très riche.

La Distribution géographique des Chalcididae (Hymenoptera)

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RÉSUMÉ

Il n'est pas sans intérêt de présenter une esquisse de la distribution géographique des Chalcididae, plus souvent récoltés et mieux étudiés que les autres Chalcidiens en raison de leur grande taille.

Les Chalcididae sont divisés en 5 sous-familles très différentes, parfaitement caractérisées par la structure du pétiole abdominal.

La comparaison des faunes des deux contrées les mieux explorées de la région holarctique, l'Amérique du Nord et l'Europe, met en évidence l'épanouissement des Chalcidinae dans le Nouveau monde. Cet épanouissement paraît s'accompagner d'une réduction du nombre d'autres Chalcididae, comme les Haltichellinae.

Si les Brachymeriinae de la tribu des Brachymeriini offrent un exemple de distribution très vaste et régulière, les tribus plus spécialisées des Phasgonophorini et des Cratocentrini ont des aires de répartition plus restreintes, parfois disjointes.

Les Epitraninae sont presque uniquement localisés dans la zone intertropicale de l'Ancien monde, mais leurs parents, les Dirhininae, ont quelques représentants dans les régions holarctique et néotropicale.

Les Haltichellinae, peu abondants en Amérique, sont très riches en genres et en espèces dans le reste du monde. C'est le groupe le plus varié des Chalcididae.

La faune mondiale des Chalcidoidea demeure fort mal connue pour plusieurs raisons: non seulement ces insectes de petite taille ont été longtemps dédaignés par les récolteurs, mais encore l'étude de l'important matériel déjà réuni dans les musées a tenté peu d'entomologistes. Les Chalcididae, généralement plus grands que les autres Chalcidiens, ont été de ce fait moins négligés et c'est pourquoi il semble possible de donner dès à présent un aperçu de leur répartition géographique. Malgré l'insuffisance des renseignements concernant les faunes australienne et néotropicale, on peut se faire une idée à peu près exacte de la distribution des grands groupes de la famille.

La famille des Chalcididae a été divisée par Ashmead en 5 tribus aujourd'hui élevées au rang de sous-familles parfaitement caractérisées, ne serait-ce que par la structure et le mode d'articulation du pétiole abdominal qui répond à un type bien déterminé à l'intérieur de chaque groupe[1]. Les 5 sous-familles forment chacune un ensemble si homogène qu'il est difficile de découvrir leurs affinités et plus encore de retracer leur évolution phylétique étant donné qu'elles offrent toujours un mélange de caractères, les uns archaïques, les autres néogénétiques. Il n'entre pas dans le cadre de cette communication de traiter ce problème, mais avant d'aborder l'étude de la distribution géographique des Chalcididae, il n'est pas inutile d'indiquer les liens de parenté qui unissent ces sous-familles. Elles peuvent être groupées de la façon suivante:

(1) Chalcidinae et Brachymeriinae, voisins par les caractères morphologiques de la tête, du thorax et des pattes. Ces Chalcididae sont les seuls à posséder des pigments ptériniques (mis en évidence par la réaction de la murexide), pigments largement répartis chez les Chalcidinae, mais uniquement localisés dans les pattes et les tegulae chez les Brachymeriinae.

(2) Epitraninae et Dirhininae, remarquables par leurs caractères communs "surévolués", et qui dérivent peut-être d'un Chalcidinae primitif.

(3) Haltichellinae, qu'il n'est possible de rattacher à aucune des sous-familles précédentes (tibias postérieurs d'un type archaïque).

L'évolution phylétique des Chalcididae est indépendante de celle de leurs hôtes, comme le démontre cet exemple: les espèces du genre *Neochalcis* Krb. parasitent des Hyménoptères aculéates xylicoles tandis que celles du genre très voisin, mais plus évolué, *Tanycoryphus* Cam., attaquent des Coléoptères xylophages (des observations de même nature ont été faites chez les Sphécides). C'est que, pour les Chalcididae—et la majorité des autres Chalcidiens—la niche écologique de leur victime a autant d'importance sinon plus, que leur position systématique. Il en résulte que de nombreuses espèces attaquent simultanément leur hôte ancestral et ses parasites (Ichneumonides, Braconides, Sarcophagides etc. . .) puis, ce stade "métaparasite" dépassé, vivent uniquement aux dépens d'entomophages, en stricts épiparasites.

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[1] La partie de cet exposé relative à l'étude du pétiole abdominal des Chalcididae a été publiée dans Bull. Mus. Nat. Hist., Paris (2) 29: 315-322. 1957.

CHALCIDINAE

La faune holarctique des Chalcididae a été suffisamment étudiée pour que l'on puisse considérer que peu d'espèces restent encore inconnues, d'une part en Amérique du Nord (Mexique exclu) et, de l'autre, en Europe (moins l'U.R.S.S.)(2).

En comparant les faunes de ces territoires (Fig. 1) il apparaît immédiatement que si les Brachymeriinae et les Dirhininae sont à peu près représentés par le même nombre d'espèces de chaque côté de l'Atlantique, les Chalcidinae dominent le Nouveau monde. On a, en effet, recensé 53 espèces de ce groupe, dont 39 *Spilochalcis* Thoms., aux Etats-Unis et au Canada, contre 4 en Europe (1 *Spilochalcis* et 3 *Chalcis* F.). Les deux faunes possèdent d'ailleurs un élément commun, le *Spilochalcis xanthostigma* (Dalm.) qui parasite, le fait mérite d'être souligné, des larves d'*Arge*, un des rares genres de Tenthrède presque ubiquistes. Les Chalcidinae, déjà si abondants en Amérique du Nord, le sont davantage en Amérique du Sud et, pour cette raison, quelques auteurs ont avancé que le centre d'origine de cette sous-famille devait être la région néotropicale. Le principe suivant lequel le centre de différenciation coïncide avec celui de la densité maximum est souvent en défaut et l'on pourrait simplement considérer l'Amérique du Sud comme un continent refuge pour ce groupe d'origine holarctique. Pour le moment, la rareté des documents paléontologiques ne

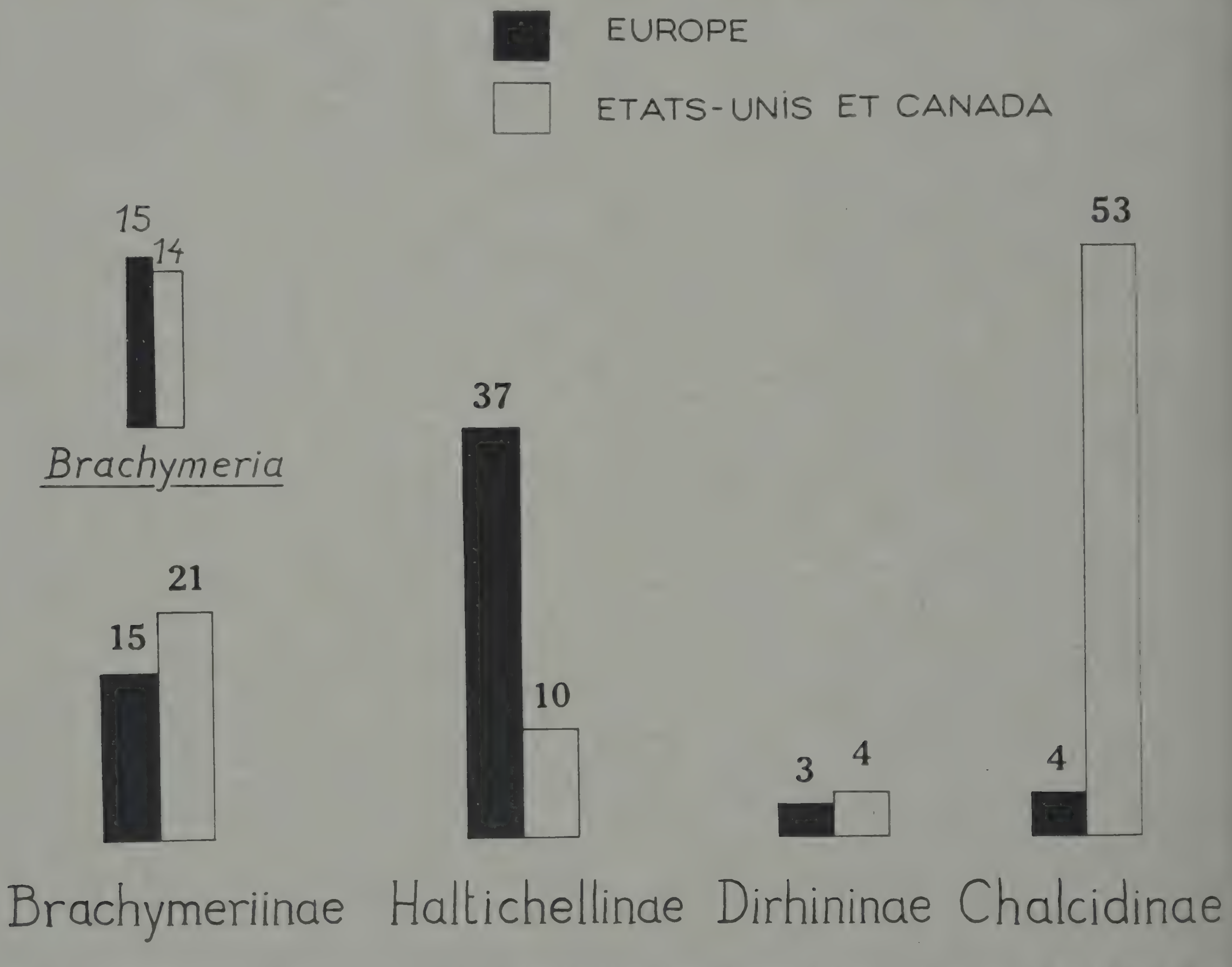

Fig. 1. Répartition numérique des sous-familles de Chalcididae en Europe et en Amérique du Nord (les chiffres indiquent le nombre d'espèces).

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[2] Une faune des Leucospidae et Chalcididae de l'U.R.S.S. est actuellement préparée par Madame M. N. Nikolskaja.

permet pas de résoudre ce problème[8], mais, quoiqu'il en soit, l'épanouissement des Chalcidinae en Amérique ne doit pas être sans rapport avec la pauvreté de ce continent en Haltichellinae et peut-être en Epitraninae.

Très mal représentés dans la région paléarctique, les Chalcidinae ne le sont pas mieux dans les régions éthiopienne ou orientale et semblent même absents de la région australienne.

La majorité des Chalcidinae parasite des Lépidoptères, mais un certain nombre d'espèces s'attaquent aux Coléoptères, aux Diptères et aux Hyménoptères, généralement des Ichneumonides ou des Braconides qui vivent eux-mêmes aux dépens de Lépidoptères. Une espèce néotropicale, *Spilochalcis patagonica* Blnchd., attaquerait indifféremment un Psychide et l'un de ses parasites, *Psychidosmicra australis* Blnchd., un autre Chalcidinae. Ce parasitisme occasionnel ou constant d'un Chalcidien par une espèce parente, voire congénère, s'observe également chez les Eurytomidae et les Torymidae (le phénomène est plus complexe chez les Aphelinidae).

BRACHYMERIINAE

La sous-famille des Brachymeriinae a été divisée en trois tribus. La plus riche, celle des Brachymeriini, est essentiellement représentée par le genre *Brachymeria* Westw., qui recrute la plupart de ses hôtes, soit parmi les Lépidoptères, soit parmi les Diptères ou les Hyménoptères entomophages. Ce genre, en apparence très peu spécialisé, réunit des espèces souvent difficiles à reconnaître en raison de la pauvreté et de la faible variabilité des caractères morphologiques, mais cette monotonie dans les formes est heureusement rompue par la diversité de la coloration, d'ailleurs sans grande signification phylétique. On peut tenir ce genre *Brachymeria* pour très réussi, car il se rencontre sur tout le globe où ses espèces sont aussi nombreuses que communes, particulièrement dans les contrées chaudes.

La région néotropicale, à la faune si singulière, possède en dehors des *Brachymeria* typiques, des formes à corps velu, ou d'autres caractérisées par un abdomen allongé en un style parfois démesuré (genre *Thaumatelia* Krb.). L'une de ces espèces, provisoirement classée dans le genre *Brachymeria*, *B. pyramidea* (F.), a été obtenue à diverses reprises du nid d'*Epipona tatua* (Cuv.). Il est possible que plusieurs de ces étranges Brachymeriini soient inféodés au biotope exceptionnel offert par les nids de Polybiines sud-américaines, attaquant soit les Guêpes, soit leurs parasites ou commensaux. La faune australienne renferme également des *Brachymeria* assez différentes de celles des régions voisines, mais ces espèces sont rarement représentées dans les Musées européens et les descriptions ne nous renseignent guère à leur sujet.

La tribu des Phasgonophorini comprend des formes parasites d'insectes xylophages, à thorax sculpté de rides transverses formant râpe, comme celui des Cynipides de la famille des Ibaliidae aux moeurs semblables. Un premier groupe des Phasgonophorini le "groupe *Phasgonophora*" se caractérise par son abdomen à premier tergite très développé, le dernier étant rectiligne comme la tarière qu'il engaine. Le genre *Trigonura* Sich., le plus riche, ne demeure inconnu que dans la région paléarctique alors qu'il possède quatre représentants dans la région néarctique où l'on rencontre encore la seule espèce du genre *Phasgonophora* Westw. (un *Trigonura* à caractères outrés). La seconde section, le "groupe *Stypiura*", réunit des formes dont le premier tergite abdominal est réduit et le dernier courbé à l'apex comme la tarière. Ce groupe se trouve uniquement localisé dans les régions néotropicale et orientale, et les biogéographes wegnériens verraient là un exemple typique de "ségrégation centrifuge inabrésienne". Les genres les mieux représentés, *Stypiura* Krb. (9 espèces de l'Amérique centrale et méridionale) et *Megalocolus* Krb. (6 espèces distribuées de la Birmanie à la Nouvelle Guinée) seraient absolument identiques si les deux premiers tergites abdominaux libres chez *Stypiura*, n'étaient fusionnés chez *Megalocolus* (Fig. 2)!

La tribu très spécialisée des Cratocentrini qui réunit les plus grands des Chalcidiens —leur taille dépasse parfois 20 mm.—ne renferme également que des parasites de xylophages appartenant à l'ordre des Coléoptères, une même espèce attaquant indifféremment des Cérambycides, des Buprestides, des Bostrychides, etc. . . La région Ethiopienne, notamment l'Afrique australe, orientale et Madagascar, semble la plus riche en Cratocentrini avec les genres endémiques *Marres* Walk., *Larradomorpha* Stadl. et quelques autres encore inédits, auxquels s'ajoutent *Cratocentrus* Cam. et *Acanthochalcis* Cam. (s. genre *Trypanochalcis* Steff.), au total une douzaine d'espèces. Deux représentants du genre *Cratocentrus*

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[8] *Eterochalcis scudderi* (Brues) du Miocène de Florissant est la seule forme fossile connue.

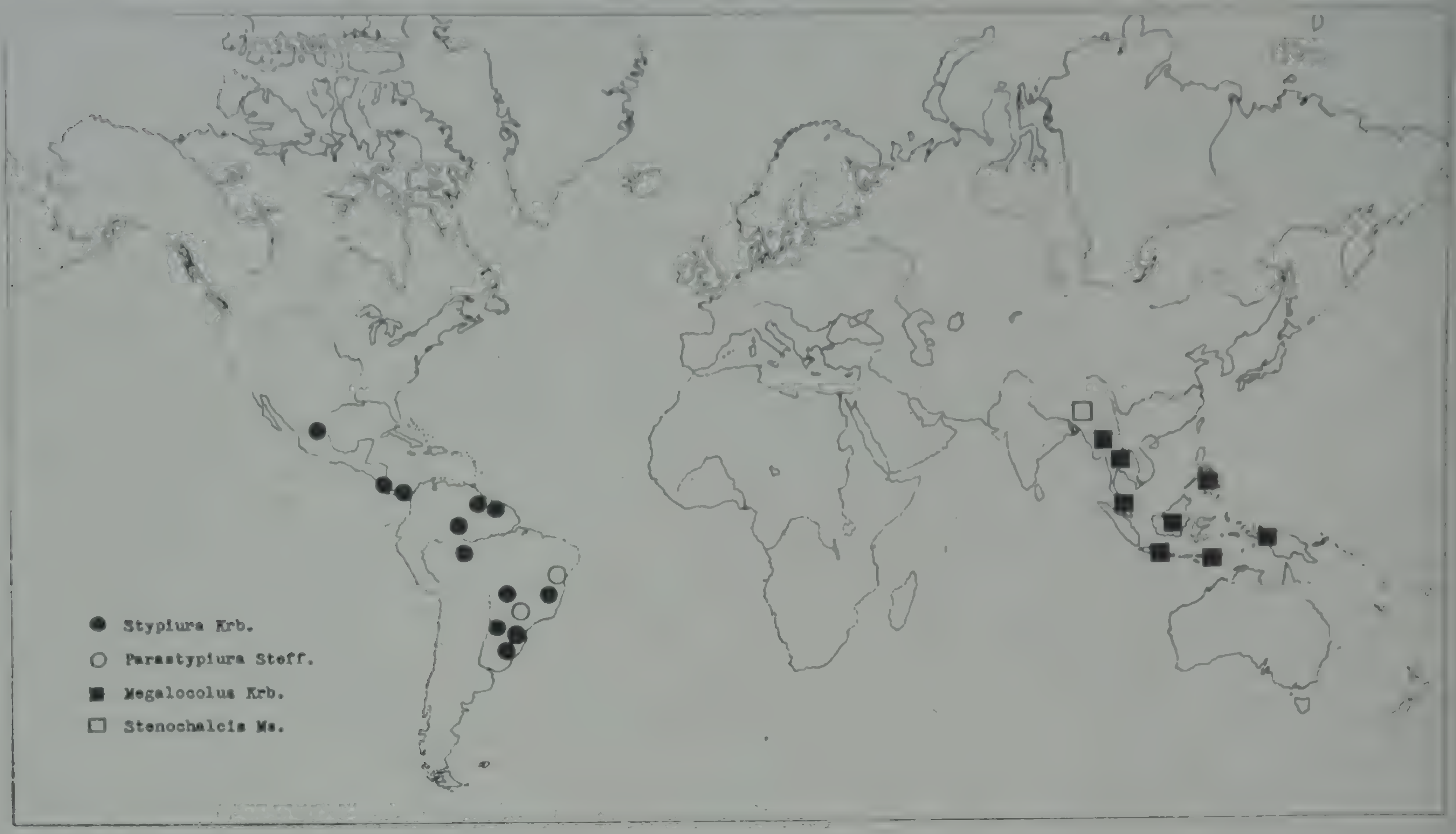

Fig. 2. Distribution des Phasgonophorini du "groupe *Stypiura*".

se retrouvent dans la région paléarctique (sous-région méditerranéenne), l'un en Afrique du Nord, l'autre en Iran. En dehors de la région éthiopienne et des territoires limitrophes, les Cratocentrini ne sont connus que dans la région néarctique (sous-région sonorienne) où se trouvent localisés deux *Acanthochalcis s. str.*, et dans la région orientale qui possède un genre bien particulier, *Allocentrus* Cam., groupant quatre espèces. Aucun Cratocentrini n'a été signalé dans la région néotropicale où les Phasgonophorini sont si abondants.

EPITRANINAE

Les Epitraninae constituent une petite sous-famille ne renfermant actuellement que l'unique genre *Epitranus* Walk., le premier décrit et le seul accepté par les systématiciens. Ce genre trop vaste mériterait d'être fragmenté, mais à la condition d'établir des coupures génériques assez différentes de celles proposées par les anciens auteurs. Les *Epitranus*, dont les très rares hôtes connus sont des Lépidoptères, paraissent presque exclusivement cantonnés dans la zone intertropicale de l'Ancien monde. Jusqu'à ces dernières années, il n'y avait que les régions australienne et orientale qui semblaient riches en espèces, mais les récentes prospections du Congo Belge et de Madagascar ont montré que la faune éthiopienne ne le cède en rien à celles de l'Australie ou de l'Extrême-Orient. En revanche, les Epitraninae doivent être mal représentés dans la région néotropicale d'où l'on ne signale que trois espèces. La région holarctique, à l'exception du Japon méridional, ne possède aucun *Epitranus*.

Entre les Epitraninae et les Dirhininae se placent deux genres étranges de la région orientale qui, en dehors de certaines particularités, offrent un mélange des caractères des sous-familles qui les encadrent. Masi avait proposé de créer pour ces Chalcididae la tribu des Aplorhini (ou sous-famille des Aplorhinae). Un seul des genres, *Aplorhinus* Ms., a été décrit, représenté par l'unique espèce, *A. bakeri* Ms., de Bornéo. Le second, resté inédit, provenant des Philippines.

DIRHININAE

La petite sous-famille des Dirhininae réunit une soixantaine d'espèces réparties entre six genres assez peu différents les uns des autres pour que l'on ait proposé de n'en conserver que le plus ancien, *Dirhinus* Dalm. Tous les Dirhininae sont probablement parasites de Diptères et plusieurs de leurs curieux caractères, notamment ceux de la tête, rappellent par convergence ceux des Proctotrypides de la famille des Diapriidae qui attaquent les mêmes hôtes. Si la distribution des Dirhininae se rapproche de celle des Epitraninae, elle est plus régulière puisque la sous-famille se trouve représentée dans les cinq grandes régions biogéographiques. Cependant les régions australienne, orientale et éthiopienne semblent une fois encore plus riches en espèces que la région néotropicale qui possède le seul genre nettement aberrant, *Hontalia* Cam., et les sept formes présentes dans la région holarctique y sont uniquement localisées dans ses zônes les plus chaudes (sous-régions méditerranéenne et sonorienne).

HALTICHELLINAE

Si la faune néarctique est incomparablement plus riche en Chalcidinae que la faune paléarctique, la situation est renversée en ce qui concerne les Haltichellinae représentés par 37 espèces en Europe contre 10 environ en Amérique du Nord (Fig. 1). Les données relatives à la région néotropicale sont très rares, mais leur pauvreté autorise à penser que la faune sud-américaine est aussi peu abondante que celle de l'Amérique du Nord.

A cette première disproportion paraît s'ajouter un second déséquilibre dans la composition même de ces deux faunes. En effet, près de la moitié des Haltichellinae d'Europe (15 sur 37) font partie de la tribu la plus évoluée, celle des Hybothoracini, tandis qu'une seule espèce de ce groupe—le type du genre américain *Schwarzella* Ashm.—a été signalé dans la région néarctique. Il existerait cependant (Burks *in litt.*) quelques Hybothoracini encore inédits dans la sous-région sonorienne, dont certains caractères climatériques répondent aux exigences de cette tribu.

Quoique la plupart des espèces nord-américaines aient été placées dans des genres primitivement décrits d'Europe, leur diagnose semblerait indiquer qu'elles appartiennent plutôt à des genres endémiques. Bien entendu, une révision de la faune néarctique permettrait seule d'élucider ce problème. Quant aux formes néotropicales que nous avons pu examiner, elles sont notablement différentes de celles de l'Ancien monde. Aussi c'est avec surprise que l'on découvre que le genre *Aspirhina* Krb., créé par une espèce brésilienne, se retrouve en Afrique australe et orientale où sont distribuées des espèces extrêmement voisines du génotype, et que *Notaspidium* D.T., représenté aux Antilles et au Mexique (Burks *in litt*), possède également de proches parents en Indo-Chine (les caractères très particuliers de ce dernier genre et de ses alliés leur interdisent d'être placés dans l'une des deux tribus existantes: Haltichellini et Hybothoracini).

Une très grande richesse en genres d'Haltichellinae caractérise l'Ancien monde, richesse qui ne résulte pas d'une multiplication artificielle des coupures génériques, mais traduit simplement l'existence d'une incomparable variété de formes. Ainsi la faune paléarctique comprend au moins 17 genres d'Haltichellinae presque exclusivement localisés dans la sous-région méditerranéenne, alors que les autres sous-familles n'en réunissent pas plus de 4! En dépit de cette abondance des genres et des espèces (66 pour l'ensemble du bassin méditerranéen), la population totale des Haltichellinae semble occuper une place relativement médiocre dans la faune paléarctique, leurs représentants étant en général peu communs, sinon rares. Il n'est pas impossible que cette rareté soit due au fait que l'on ignore encore presque tout de la biologie des Haltichellinae, dont les quelques hôtes connus appartiennent à des ordres aussi éloignés les uns des autres que les Lépidoptères et les Strepsitères, ou les Hyménoptères et les Névroptères. Mais, cette réserve faite, il demeure qu'au cours des "chasses entomologiques", on récolte beaucoup moins d'Haltichellinae que de *Brachymeria*, comme le prouve l'examen des collections.

Sur les 17 genres d'Haltichellinae de la faune paléarctique, 7 sont endémiques (5 Haltichellini et 2 Hybothoracini), les 10 autres, très largement distribués, se retrouvant simultanément dans les régions éthiopienne et orientale (6 Haltichellini et 4 Hybothoracini). La densité des espèces dans le bassin méditerranéen indique clairement que celui-ci a été envahi par l'Est.

Les deux régions éthiopienne et orientale, beaucoup plus riches en Haltichellini, posséderaient chacune environ un tiers de genres endémiques et deux tiers de genres communs. Les contrées tropicales sont encore si mal prospectées que, calculées en tenant compte de très nombreuses espèces inédites conservées dans les musées, ces proportions peuvent être néanmoins contestées. Il est toutefois certain que ces faunes européenne, africaine et asiatique sont, dans l'ensemble, voisines et peut-être ne diffèrent pas essentiellement de la faune australienne bien pourvue en Haltichellini des groupes *Hockeria* Wlk. et *Antrocephalus* Krb. Parmi les genres endémiques australiens, il s'en trouve un très voisin du genre *Allochalcis* Kieff., localisé à Madagascar: *Trichoxenia* Krb.

La tribu des Hybothoracini qui constitue un élément essentiel de la faune méditerranéenne (28 espèces sur 66) paraît assez mal représentée dans les régions tropicales humides.

Ainsi, dans les collections du Musée de Tervuren, pour environ 200 Haltichellini congolais répartis en une cinquantaine d'espèces, on compte seulement 12 Hybothoracini appartenant à 3 espèces. En Afrique australe et dans les zônes sahélienne et soudanaise de l'Afrique occidentale, les Hybothoracini reprennent une place non négligeable dans la faune locale. Une telle distribution semble naturellement due au fait que la plupart des espèces de cette tribu sont xérophiles et psammophiles, ainsi que l'indique leur biotope en Europe[4]. Mais, paradoxalement, ce sont ces mêmes Hybothoracini que l'on rencontre sous les latitudes les plus différentes: *Lasiochalcidia guineensis* Steff., décrit de Guinée, a été retrouvé en Europe centrale et méridionale; *L. differens* Bck., décrit de Palestine, a par la suite été récolté au Sénégal, puis au Congo belge; *Invreia propinqua* Steff., du Congo belge et de la Rhodésie du Sud, considéré a priori comme une espèce valide en raison de sa distribution géographique, n'est peut-être qu'une simple variété de l'espèce européenne *I. ligustica* Ms.! Une telle indifférence à la température a déjà été signalée chez les Hyménoptères supérieurs (Sphécides, Vespides) dout les Chalcididae—peut-on écrire en guise de conclusion—se rapprochent manifestement par leur mode de répartition.

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[4] Au moins quatre de ces Hybothoracini psammophiles, appartenant aux genres *Hybothorax* Ratz. et *Lasiochalcidia* Ms., parasitent des Fourmilions dans les régions paléarctique, éthiopienne et orientale. Mais deux Haltichellini attaquent les mêmes hôtes en Amérique du Nord et aux Indes et l'on peut se demander si ce choix n'est pas la conséquence d'une incapacité au vol soutenu: dans la région méditerranéenne, c'est sur le sol que j'ai le plus souvent récolté des Hybothoracini; *Euchalcidia nigripes* (Fons.) dont l'hôte naturel est inconnu, a été capturé dans des nids d'araignées lapidicoles; l'espèce éthiopienne *E. caryobori* Hanna, parasite des *Caryoborus* et des *Pachymerus* qui se développent dans des graines de légumineuses tombées à terre.

Contribution Towards a Monograph of the Oedemeridae II. Speciation and Distribution in the Genus *Oxacis* (Coleoptera)[1]

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The genus *Oxacis* contains about forty species in the Nearctic and the northern part of the Neotropical Region, plus thirty-four unrecognizable species from South America. The latter are all described by Pic and remain unknown to the author at the present time. The genus is essentially tropical and subtropical, with the center of distribution in Mexico and Southwestern United States, with a few species extending down the west coast of South America into Chile and over into Argentina.

The extremely variable nature of the morphological features of this genus makes it one of those many problem genera and cannot be classified satisfactorily without the help of ecological and life history data. The genus gives every appearance of being in a state of active speciation. Almost all of the known species have overlapping ranges. The barrier between species, where determined, are ecological and not, or seldom, geographical. Museum study of the species can be done only with great difficulty and, therefore, most of the species cannot be adequately characterized until more extensive field studies are made. This paper is the result of several years of laboratory study in preparation for this contemplated field work.

SUMMARY

Obviously significant distribution patterns are apparent in the genus *Oxacis*. The life history of these beetles, as now known, do not indicate a direct relationship with certain flora types, i.e., they are not host specific to certain plants, or certain flora types. This is seen when the distribution patterns are compared with the Biotic Provinces of Dice which are based on floral types. However, there is a distinct ecological relationship evident in these distribution pictures because in almost all cases the range of the species are confined to similar Biotic Provinces and do not extend beyond these groups of Provinces into the edge of other Provinces except in very few cases.

The present status of the study is: a) Most of the species are morphologically closely similar; b) the characteristics used to separate the species are variable, but they can be separated in 95 to 98 percent of the cases; c) distribution patterns conform to Dice's Biotic Provinces in nearly all cases so far studied; d) before the study of the genus can be satisfactorily concluded, field studies of individual local populations and single broods must be made, and life history data accumulated.

I believe this to be an excellent example of the limitations of the usual museum type study of dried insects collected by the usual mass accumulation of specimens at light or by sweeping. Such methods of course are necessary as a start, but in this group, at least, it is time for some painstaking field work.

CHARACTERISTICS OF THE GENUS

This genus has recently been restricted (Arnett, in press) by raising the subgenera *Oxycopis*, *Xanthochroina*, and *Paroxacis* to generic rank. The details of this classification are dealt with elsewhere (Arnett, 1951 and in press). The genus *Oxacis* as now recognized, is characterized by entire mandibles, claws without a basal tooth, apical tibial spurs 2–2–2, eyes large and slightly emerginate near point of insertion of the antennae. Pubescence, sculpturing, and color are variable with the species, and within the species. Each of these simple features must be further considered for some understanding of the species included in the genus.

The male genitalia of most of the genera of Oedemeridae are very useful for the characterization of species. All of the genera known to the writer may be defined on the basis of the characters found in the male genitalia, including the genus *Oxacis* (see Arnett, 1951). However, the male genitalia of this genus show no characteristics of use for the separation of species; in fact, they are remarkably uniform for this family.

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[1] The previous part of this series, no. 10, was published in *The Coleopterists' Bulletin* 10: 57-60, 1956.

The mandibles are of three types for the family: 1) apices bifid, 2) apices entire, or 3) apex of the right mandible bifid. They are entire in *Oxacis*, but may be large, curved posteriorly, and blunt at the apices (*O. trimaculata*), varying to short, straight, and acute at the apices. There is considerable variation in these characteristics within the species, but, coupled with other features, the shape of the mandibles, even though variable, are useful for specific definition.

The presence or absence of a small, basal tooth on each claw appears in widely separated genera. So far as is now known, this characteristic is always generic, and is not subject to variation.

The apical spurs on the anterior tibiae may be either absent, one, or two. Although this is still treated as a generic characteristic, it is evidently a subfamily character.

The size and shape of the eyes appear to have generic value, but it is difficult to describe these features in words. Ratios are more indicative. The distance between the eyes has some value in defining species where described in ratios. These features are somewhat variable also.

The species of this genus are defined most easily by a description of the sculpturing, pubescence, and color combinations, in spite of the great variation of these features within the species. This will be discussed in detail below. However, it should be pointed out that the problem in the classification of the species of this genus on a morphological basis lies here. The necessity of using such notoriously variable features as these means that additional data must be employed before a sound classification can be constructed. Whenever such genera are encountered, the systematist must turn to geographical distribution, ecology, life history, and habits before he can be sure that his classification is based on sound principles. It is these aspects of the classification of this genus that are of general interest.

VARIATION IN SPECIFIC CHARACTERISTICS

When this problem was first investigated by Horn (1896) so few specimens were available that the variation was not suspected. When my revision of the Nearctic species (1951) was undertaken (under the able direction of the chairman of the present session) in 1947 there was enough material available so that it was easy to see that much more was needed before the genus could be understood. I have since been able to study several thousand specimens, and I feel that I am beginning to understand something of the processes involved in the speciation herein. Before further revisional work can be done, it will be necessary to study local populations. I think this is a good example of a problem so often attempted by museum style taxonomy, but that can be solved only by careful field work on the part of the reviser himself.

First studies seemed to indicate that the genus was composed of three or four well defined species plus one very abundant, variable, and widely distributed species. Attempts were made to arrange the specimens in such a manner as to reflect a correlation between geographical range and morphological features. These attempts failed entirely and seemingly indicated wide local variations in color, sculpturing, and pubescence. Series bearing the identical locality and date label showed very little variation, but series collected in the same locality at another date and by other collectors were considerably different. Certainly very detailed notes on the habitat of each specimen would be very helpful.

A large collection of oedemerids from the Bimini Islands, Bahamas, were sent to me for study by the American Museum of Natural History. The restricted area, and the several years of collecting involved gave me valuable clues to the expected variation of these species (Arnett, 1953). The results of this experience was then applied to *Oxacis* as a whole. I think it is now possible to separate the species of the genus with reasonable accuracy. The several characteristics used for the separation of the species must always be used in combination so that few clear-cut key characteristics are available. When this is done, however, geographical patterns become evident. These specific characteristics are elaborated below.

1. Because color combinations are prominent, these will be discussed first. Three dominant patterns are evident: (a) dark bluish or greenish metallic, lead-colored, or black. Species of these colors show little variation, and are among the easiest to define. (b) Reddish orange with dark elytra. This is the most frequent color combination, and the most variable. I am guessing that this is the color pattern of the original stock, and that it is this stock

that is responsible for the population pressures that may eventually result in additional species. These forms are the most variable, and hence the most likely to have the genetic potential for the production of additional species if they are pushed into some ecological niche and survive isolated from the main stock. However, there is practically no evidence at the present time of such a process taking place. (c) Brown to pale tan or yellowish; these species include both the best defined, and the most poorly defined species. A few of the yellowish species are distinctly marked with black stripes. The remainder of the brown species are very difficult to define because of variations in shape and pubescence.

2. Pubescence differences are as variable as color. Three features are evident: (a) pubescence uniform in color. This is the usual condition. There are at least two species (*O. variegata* Champion), and one undescribed species that have (b) bicolored pubescence. One of the species is known from so few specimens that little can be said of its variability. The other is poorly defined on the basis of color differences of the pubescence. Many specimens show this feature, but in every series there are a few specimens that have uniform coloration, and all large series have a range varying from equal parts of both colors to a very few erect, brown hairs scattered throughout white decumbent hairs. A few species have (c) very coarse, dense pubescence (*O. pallida* (LeConte) and *O. sericea* Horn). This character shows little variation and is a good diagnostic feature. A few additional species (*O. laevicollis* Horn and *O. nitens* Arnett) have very fine, sparse pubescence and this is also a good diagnostic characteristic. The normal condition is fine, short, decumbent pubescence that neither obscures the sculpturing nor exposes the sclerites.

3. Finally, features of the sculpturing offer some diagnostic characteristics. The sculpturing of the ventral surface is nearly uniform throughout the genus. The diagnostic features of the sculpturing are confined to the dorsal surface of the head, pronotum, and elytra. They are extremely variable and subtle. They must be used only in combination with other characteristics. Some species have fairly large and distinctly formed punctures, well separated, with smooth areas between (*O. nitens*). The number of punctures per square millimeter is useful information. Other punctures are shallow and indistinctly formed; still others, even though deep, are so close together that they form a rugose-punctate surface. The area between punctures may be smooth, or micro-rugose, that is, with a very fine rugose surface visible at about 100X. These variations in sculpturing are very constant in some species, whereas other species will have individuals that show all of these variations except for the smooth, sparsely punctate surface.

DISTRIBUTION TYPES

It is understandable of course that most terrestrial distribution studies have been made on vertebrates and plants and that our general knowledge of distribution has been made from these data. It is equally evident that such generalizations are weakened by the lack of invertebrate data, and that any detailed studies on terrestrial invertebrates should serve to contribute to the clarification of distribution theory. That such studies are steadily increasing is gratifying to students of distribution, even if, as is often the case, they are buried in the specialized taxonomic literature.

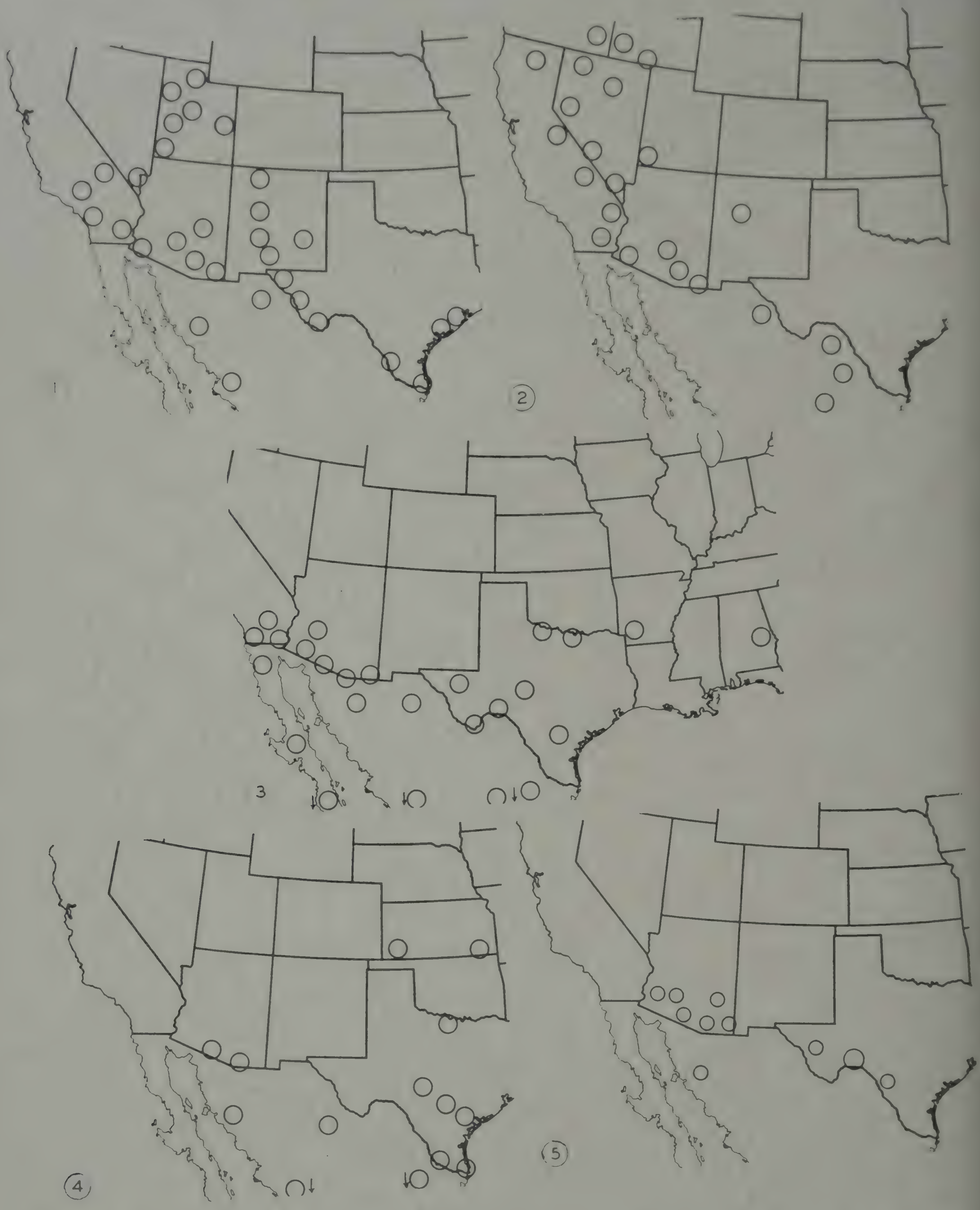
Of the four classification of communities discussed by Dice (1952), the most convenient for the purpose of this paper is the Biotic Province classification. These were characterized in some detail by Dice (1943) and all following discussions are based on these descriptions where described by him. They are useful because they give a clue to the habitat preference of the species involved.

1. *Oxacis pallida* (LeConte)

Fig. 1

Distribution. Eastern edge of Artemisian, east central part of Californian, Mohavian, southern Navahonian, Sonoran, Apachian, northern Chihuahuan, Tamaulipan, and coastal, western Austroriparian. This is one of the four species found east of the Texan Province.

Discussion. This species is very uniform throughout the range. The biology is unknown, and no data are available to me to show any habitat correlation. I would suspect that there is some relationship between this species and sagebrush. The only real inconsistency in this distribution pattern is the presence of the species in the lower Rio Grande region and the eastern coastal area of Texas.



Figs. 1–5. Distribution of *Oxacis* spp. Arrows indicate range extends farther south. 1, *pallida* (LeConte). 2, *sericea* Horn. 3, *trimaculata* Champion. 4, *championi* Arnett. 5, *cana* LeConte.

2. *Oxacis sericea* Horn

Fig. 2

Distribution. Palusian, Artemisian, Californian, Mohavian, Sonoran, Apachian, Navahonian, and Chihuahuan.

Discussion. This is closely related to, but distinct from the preceding species. It is only slightly variable. The range of the two species is very similar except that this species extends further north into the Palusian Province, a province similar to the Artemisian, and does not extend into the Tamaulipan and Austroriparian provinces. Despite its abundance, the biology is also unknown, except that it has been taken by beating Juniper.

3. Additional Wide Range Types

Two additional species show the same wide range as *O. sericea*; these are *Oxacis trimaculata* Champion and *O. championi* Arnett. Both of these species are extremely variable and quite distinct from each other. *O. trimaculata* (Fig. 3) shows some interesting correlations. The specimens from the eastern part of the range, Austroriparian, Comanchian, and Chihuahuan (no specimens are known from the Texan Province) are large and reddish, except for specimens from Terrell County, Texas, and the specimens from Alabama. The Arizona specimens are extremely variable. The California specimens lack spots on the pronotum, despite the name. Additional data might confirm my suspicion that at least three subspecies are involved here. Lack of precise habitat data prevents me from making these divisions at the present time.

The other species, *O. championi*, is extremely variable throughout its extensive range (Fig. 4), with specimens rare from the periphery of the range so that nothing as yet can be said about any subspeciation.

4. Restricted Range Species

Two species, *Oxacis cana* LeConte (Fig. 5), the type of the genus, and *O. granulata* LeConte (Fig. 6), show a distribution pattern that may be close to that of the original stock. *O. cana* was once thought to be the most abundant and widely distributed species in the genus. Its range is principally southern Arizona, with less dense populations extending along the upper Rio Grande valley. A few specimens are known from Sonora. Once the other species had been separated from this species, it was apparent that the populations showed little variation.

Oxacis granulata has a range basically the same as *O. cana*, but has extended into California, the lower Rio Grande valley, and farther into Sonora. It is somewhat more variable than *O. cana*, but shows no correlation between the variation and portions of the range.

5. *Oxacis niticollis* Champion

Fig. 7

Distribution. Sonoran and Chihuahuan.

Discussion. Even though these two provinces are widely separated, the specimens available of this species are remarkably uniform. There are obviously two possibilities here. Either further collecting will fill in the gap in the range, or this represents the remains of a once broader range. This range has the same elements found in the preceding example.

6. *Oxacis minuta* (Champion)

Fig. 8

Distribution. Sonoran and Chihuahuan.

Discussion. The same distribution is evident here as seen in the preceding species, but here, instead of morphological uniformity, three forms appear to be present. The southern Mexican specimens are much darker than those from Arizona and Baja California. The Rio Grande valley population shows differences in the shape of the pronotum. Here again, the lack of adequately documented material seems to indicate that the description of these as subspecies is premature.

7. *Oxacis nitens* Arnett

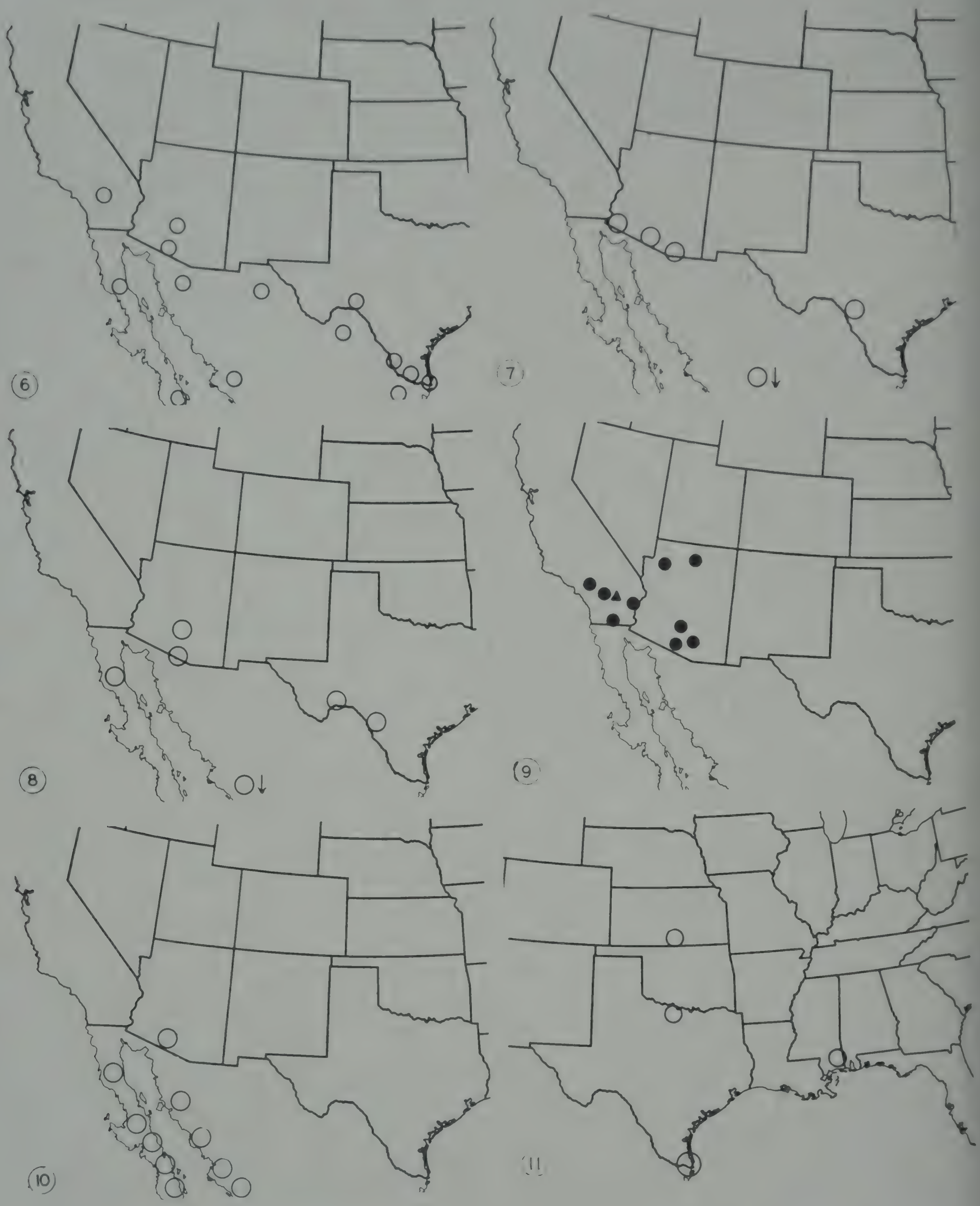
Fig. 9

Distribution. Mainly Mohavian, but extending into Sonoran and Californian Provinces.

Discussion. A clear cut subspecies is apparent near the center of the range of this species. Morphological and ecological evidence separates *O. nitens nitens* from *O. nitens knulli* Arnett. The type subspecies is a lowland form, found in canyons and desert regions. The other known subspecies is a mountainous form, found on the upper meadows of the Santa Rosa Mountains of California.

8. Aberrant Range Types

Three species in particular show a considerable shift from the basic range pattern exhibited by *O. cana*. *Oxacis rugicollis* Champion (Fig. 10) is restricted to the lower part



Figs. 6–11. Distribution of *Oxacis* spp. Arrows indicate range extends farther south. 6, *granulata* LeConte. 7, *niticollis* Champion. 8, *minuta* (Champion). 9, *nitens nitens* Arnett (circle) and *nitens knulli* Arnett (triangle). 10, *rugicollis* Champion. 11, *barbara* Arnett.

of the Californian, the Sonoran, and the Sinaloan Provinces. This species still is found in the supposed center of distribution in southern Arizona. Another species, as yet undescribed, is known only from southern California, Baja California, and one locality in Sonora, representing a western shift. *Oxacis barbara* Arnett has moved to the east (Fig. 11) and shows two color forms, the Texas and Mississippi specimens agree. The one specimen from Kansas is distinct from the others, but obviously further study of the area is needed before any definite statements can be made about the significance of this.

Finally, two species, *Oxacis taeniata* (LeConte) (see Arnett, 1953, Fig. 1 for distribution map) and *O. laeta* (Waterhouse) are far removed geographically from the rest of the species of the genus. *O. taeniata* is known only from east coast Austroriparian, and *O. laeta* is Greater Antillian, extending from Puerto Rico through the Antillies up the Florida Keys, and has been recently discovered established in southern Florida. Both of these species are very distinct, easily separated and show little variation.

REFERENCES

Arnett, R. H., Jr. 1951. A revision of the Nearctic Oedemeridae (Coleoptera). *American Midl. Nat.* 45: 257–391.
Arnett, R. H., Jr. 1953. The oedemerid beetles of the Bimini Island Group, Bahama Islands, British West Indies. *American Mus. Novitates* No. 1643: 13 pp.
Dice, Lee R. 1943. The biotic provinces of North America. *Univ. of Michigan Press.* 78 pp.
Dice, Lee R. 1952. Natural communities. *Loc. cit.* 547 pp.
Horn, George H. 1896. The Oedemeridae of Boreal America. *Proc. California Acad. Sci.* (2), 6: 382–421.

Geographical Distribution of the Net-Winged Midges (Blepharoceridae, Diptera)

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ABSTRACT

The family Blepharoceridae is of very unusual interest, not only in the unique immature stages and life-histories of the included forms, but in the geographical distribution of the species. As here recognized, the family includes 21 genera, with 165 described species, arranged in four subfamilies. There are no known fossil species. Representatives occur in all six of the major biotic regions, including the islands of Madagascar and New Zealand, indicating a considerable antiquity for the group, perhaps to the mid-Mesozoic, or some 150,000,000 years ago. In the present treatment the four subfamilies are arranged from the more generalized to the specialized. The most primitive, the Edwardsininae, with the genera Edwardsina *and* Paulianina, *is restricted to the Southern Hemisphere. The Blepharocerinae, with six genera* (Agathon, Bibiocephala, Blepharocera, Dioptopsis, Liponeura, *and* Philorus) *is similarly confined to the Northern Hemisphere. A third subfamily, the Paltostominae, with eight genera* (Dimorphotarsa, Elporia, Hapalothrix, Kelloggina, Limonicola, Neohapalothrix, Paltostoma, *and* Tianschanella) *occurs in both the Old and New Worlds, chiefly in Tropical America and South Africa. The remaining subfamily, the Apistomyinae, with five genera* (Apistomyia, Hammatorrhina, Horaia, Neocurupira, *and* Peritheates) *is restricted to the Old World, ranging from southern Eurasia to Australia and New Zealand. The accompanying paper provides a record of all known species with their distribution, a key to the genera, and a selected bibliography.*

INTRODUCTION

The family Blepharoceridae, commonly known as the net-winged midges, is one of the most distinct and isolated groups within the Diptera, being exceptionally well defined in every stage from larva to adult.

As at present known, the family includes only about 165 species in 21 genera, arranged in four subfamilies. From its virtual world-wide distribution, including the islands of Madagascar and New Zealand, it must be of considerable antiquity, probably dating from the mid-Mesozoic, or perhaps 150,000,000 years ago. Unfortunately there is no fossil record for the family. The two such genera named by Cockerell and assigned to the Blepharoceridae are believed to pertain to other Nematocerous groups, *Paltostomopsis* (1915) apparently being a Tipulid, while *Philorites* (1920) is held by Edwards as possibly belonging to the Bibionidae, in the vicinity of *Plecia*. From present evidence, the family originated in the Southern Hemisphere.

Despite the fact that members of the family are relatively common and are well-known both in Europe and in eastern North America, where early work on entomology had been done, no species was made known until the early 1840's when representatives of two European genera were described at almost the same time, by Westwood (1842), Macquart (1843) and Loew (1844).[2]

The peculiar secondary folding or netting that has given to the group its familiar name was noted at virtually the same time (1862) by Bigot in *Apistomyia* and by Loew in *Blepharocera*. The latter's observations are of unusual interest, particularly when it is realized that nearly twenty years were to pass before they were confirmed by the discovery of the early stages. "Besides the longitudinal veins, the wings show some fine cracks, perfectly similar in both, and looking as though produced by the expansion of the wings, which had previously been folded; this mark is peculiar to them, pointing to some peculiarities in their transformation unfortunately still unknown; some certainty about the place due to them in the system may, therefore, be expected from the knowledge of their earlier stages."—Loew (1862: 8).

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[1] Contribution No. 1222 from the Department of Entomology, University of Massachusetts.

[2] Dates in parenthesis, in almost all cases, refer to citations in the references or else in the lists of genera and species in the text.

Both the larvae and the pupae are attached to submerged stones in swift-flowing streams or rapids, often under almost torrential conditions. It is surprising that the very distinctive larvae and pupae were not found by the early naturalists, since they often are common and readily observed. The first discovery of the early stages was by Fritz Müller, in Santa Catharina, Brazil, and his account (1879) led almost at once to the finding of these stages in Europe by Dewitz and Wierzejski, and in North America by Riley, all in 1881.

Early accounts by Müller (1881) indicated a peculiar trimorphism in the species that he described as *Paltostoma torrentium* (now in *Dimorphotarsa* Lutz), with males having holoptic heads and with two distinct types of females, one being holoptic and nectar-feeding, the other dichoptic and blood-sucking. Although Müller made no statement that his term 'sanguisugous' pertained to mammalian blood, it was so construed by various later students and the habit was recorded in various works on medical entomology for the succeeding thirty years (Sergent, 1909: 252–253; Alcock, 1911: 131; Gedoelst, 1911: 213; Surcouf, 1911: 269–273). Despite vigorous protests by Müller, contemporary Dipterologists, including Osten Sacken and Williston, questioned the possibility of such a trimorphic condition and it was gradually discredited. It is believed that since the larvae of various species may occur in a single stream habitat more than a single species was confused under the name *torrentium*. Osten Sacken (1895) believed that the females with mandibles belonged to the genus *Snowia* (now *Kelloggina*) and that the holoptic male should carry the name *Curupira torrentium* (Müller), now in *Dimorphotarsa*. Later studies by Lutz (1920) confirmed the belief that more than a single species had been so confused.

The adults of the net-winged midges are aerial and are highly elusive, often being overlooked even where the immature stages are numerous in the nearby streams. The practice of extracting the unemerged adult from the fully matured pupa was first performed by Müller and has been followed by many later students. The early belief, insisted upon by Osten Sacken (1880), that the holoptic or dichoptic condition of the head was a character of both sexes of any given species and that no Blepharocerid known to that date had holoptic males and dichoptic females, as common in some other groups of flies, was later proved erroneous (Brodsky, 1930, and several others). Similarly it was believed that the presence of mandibles was a character peculiar to the female but later it became evident that either sex may possess mandibles or these can be entirely lacking. Edwards (1929) has called attention to the fact that the mandibles either are fully-developed and functional, or else are entirely lacking, with no intermediate condition known, that is, there is no evidence of gradual atrophy of the organ.

To indicate the range of variation of characters possible within the limits of a single genus, the South African genus *Elporia* Edwards, as discussed by Stuckenberg (1955) may be cited. Number of segments in the maxillary palpus three or four; antennal segments thirteen to fifteen; mandibles present or lacking; head holoptic or dichoptic, with a noteworthy variation in the degree of bisection of the eyes; shape and armature of the tarsal claws.

VENATION AND TRICHIATION OF THE WINGS

The most readily available characters for separation of the different genera are to be found in the wings and for use in this report I am showing the venation of the known genera (Fig. 1–23). The following characters and tendencies should be noted:

Subcosta (*Sc*) is usually short, gradually becoming evanescent beyond the general level of the arculus. Its extreme length is found in *Bibiocephala* and *Agathon* (Figs. 3, 4) rather than in more primitive genera such as *Edwardsina* and *Paulianina* (Figs. 1, 2).

Radius (*R*) shows marked extremes in the number of branches, from the primitive 4-branched condition in the Edwardsininae (Figs. 1, 2) to the extreme reduction found in *Hammatorrhina* (Fig. 23), where a single branch persists, *Rs* and its branches being entirely lacking. The contention of the present writer that there is no radial crossvein (*r*) in the Diptera and that its position has been assumed by R_2 has been discussed in various earlier papers and need not be repeated here. It is of interest to note that in the Blepharoceridae not only R_2 has become so united with vein R_1 but R_3 has followed the same course, as may be seen by comparing figures 1 and 2 with 3, 4, and 5, the end result in all genera beyond the Edwardsininae being an apical fusion of R_{1+2+3}. A comparable condition is found in the Mycetophilidae. In the higher genera, where only two branches of *Rs* persist, these are R_4 and R_5 respectively. Where a single branch of the sector remains, this is R_5 and not *Rs*, as has been maintained by some writers.

Media (*M*). Confusion has resulted in the naming of the apparent crossvein (M_{3+4}) near the wing base, as shown in Figs. 2 to 9, and again in 12. Almost all recent workers have miscalled this element the *m-cu* crossvein, despite the evidence that became available with the discovery of *Edwardsina* (Tillyard, 1922, Fig. 1, a). It is likewise apparent that in all higher Blepharoceridae the vein that simulates a forked cubitus is, in reality, a composite vein, its anterior branch being the combined *m-cu* and M_{3+4}, the posterior branch Cu_1 alone (Figs. 13–23). The semiatrophied Cu_2 is rarely evident except in generalized types (*Edwardsina* and a few others). The basal connection of vein M_3 with M_{3+4} is preserved only in *Edwardsina* (Fig. 1).

Anals (*A*). A single Anal vein occurs, in the more specialized forms being partly or wholly atrophied (as *Tianschanella*, Fig. 18; *Neocurupira*, Fig. 19). The axillary thickening, found to a greater or less degree in all known members of the family, was held by Tillyard (1922) to represent a remnant of vein 2*nd A*. I am not entirely convinced that this is the true explanation.

Trichiation. Macrotrichia of the wing cells are found only in *Paulianina* (Fig. 2) and their arrangement is such that they suggest the position of formerly existing veins.

Macrotrichia of the veins range from virtually complete series on all the veins (Edwardsininae) to an almost complete loss, except on Costa, in the higher forms. It may be noted that in *Edwardsina*, some species possess an almost complete series of trichia while in others (as *E. argentinensis*) these bristles are sparse or lacking on veins R_4, branches of *M*, and the Anal vein, but recur strongly on the main stems of *M* and *Cu* basad of the arculus.

The Blepharocerinae (including *Agathon*, *Blepharocera*, most *Dioptopsis*, *Liponeura*, and *Philorus*) have trichia on C, R and its branches, the outer end of M_1 and on the free tip of M_3. In *Bibiocephala* these occur on C and the first branch of R. In some species of *Dioptopsis*, as *sequoiarum*, there are no trichia on M_3. In the more advanced subfamilies, Paltostominae and Apistomyinae, there are no trichia on the veins behind R, while in the most specialized genera, including *Apistomyia*, *Hapalothrix*, *Neohapalothrix* and *Hammatorrhina*, such trichia are virtually restricted to the costal vein.

The gradual increase in our knowledge of the taxonomy of the family is shown by the following table that indicates the known number of genera and species at various periods of time.

Author and Date	Genera	Species
Loew (1869)	4	6
Osten Sacken (1878)	7	11
Williston (1896)	9	17
Kellogg (1907)	9	20
Alexander (this report)	21	165

Undoubtedly there will be many further discoveries in the family. Since the presentation of this paper at the Tenth Entomological Congress in Montreal, August 1956, further important additions to our knowledge of species and distribution have been made. Dr. John Lane is describing some 15 additional species of *Dimorphotarsa* (as *Curupira*) from southeastern Brazil. The first record of the family in North Africa is the discovery in Algeria of three new species by F. Vaillant and the even more surprising finding of a species in French Guinea by Dr. Fernand Schmid.

KEY TO THE GENERA OF THE BLEPHAROCERIDAE

1. Four branches of Radius reach the wing margin; *Rs* with a long backward spur at origin. Subfam. I Edwardsininae Edwards, 1929 (Southern Hemisphere) 2
Fewer than four branches of Radius reach the wing margin; *Rs* without a spur. . . . 5

2. Basal section of vein M_3 preserved; no macrotrichia in the wing cells. (Fig. 1) (*Edwardsina* Alexander) 3
Basal section of vein M_3 atrophied; conspicuous rows and areas of macrotrichia in all outer wing cells. (Fig. 2) (Madagascar) . . . . *Paulianina* Alexander

3. Tibial spur formula 1-2-2; cell R_3 sessile or short-petiolate, the petiole not longer than *Rs*. (South Chile, Argentina) . . . . . . Subgen. *Edwardsina* Alexander
Tibial spur formula 1-1-1 or 1-0-1; cell R_3 long-petiolate, less than three times as long as the petiole which is several times longer than *Rs*. 4

4. All tibiae with a single spur, the formula 1-1-1. (Tasmania, southeastern Australia) . . . . Subgen. *Tonnoirina* Edwards
No spur on middle tibia, the formula 1-0-1. (Southeastern Australia, south Chile) . . . . Subgen. *Alexina* Edwards

5. Distal section of vein M_3 preserved. (Figs. 3-11). Subfam. II Blepharocerinae Bezzi, 1912 (Northern Hemisphere) 6
Distal section of vein M_3 atrophied (Figs. 12–23). 12

6. *Rs* with three branches, vein R_3 preserved as a short to longer element (Figs. 3, 4, 5). 7
Rs with two branches, vein R_3 lacking (Figs. 6–11). 8

7. Vein R_3 long, much exceeding the terminal fusion R_{1+2+3}; thoracic pleura with setae (Fig. 3). (Western North America; Japan . . . . *Bibiocephala* Osten Sacken
Vein R_3 much shorter than R_{1+2+3}, when most reduced simulating a crossvein in the axil of *Rs*; thoracic pleura glabrous (Figs. 4, 5). (Western North America; Japan) . . . . *Agathon* von Röder

8. Basal section of vein M_{3+4} preserved (Figs. 6–9). 9
Basal section of vein M_{3+4} atrophied (Figs. 10–11). 10

9. Cell R_4 sessile (Figs. 6, 7). (Western North America; Eurasia) . . *Dioptopsis* Enderlein
Cell R_4 long-petiolate (Figs. 8, 9) (Western North America; Asia) . . . *Philorus* Kellogg

10. Eyes entire and broadly separated in both sexes; middle coxa without a spur (Fig. 11). (Europe, eastward to Caucasia) . . . . *Liponeura* Loew
Eyes bisected, separated or contiguous; middle coxa with a spur (Fig. 10). . . . . (Eurasia; North America) (*Blepharocera* Macquart) 11

11. *Rs* short, less than twice *r-m*. (Eurasia; North America) . . . . Subgen. *Blepharocera* Macquart
Rs longer, approximately three times *r-m*. (Japan) . . Subgen. *Parablepharocera* Kitakami

12. Labial palpi usually small and inconspicuous, much shorter than the base of the labium, the entire organ sometimes much reduced. Subfam. III Paltostominae Bezzi, 1912 (Neotropical; southern Ethiopian; Eurasia) 13
Labial palpi unusually long and slender, glabrous, usually curved outwardly, the base of the labium similarly lengthened. Subfam. IV Apistomyinae Bezzi, 1912 (Eurasia; Australasia) 21

13. Basal section of vein M_{3+4} preserved (Fig. 12) (Neotropical). . . *Kelloggina* Williston
Basal section of vein M_{3+4} atrophied (Figs. 13–23). 14

14. Eyes bisected; maxillary palpi long, 3- or 4-segmented; claws simple or with small teeth. 15
Eyes entire; maxillary palpi 1- or 2-segmented; claws simple or with a single large tooth. 18

15. Hind tibia with a single spur (Fig. 15). (South Africa; southern South America) . . . . *Elporia* Edwards
Hind tibia with two spurs. 16

16. Antennae 15-segmented; claws simple (Fig. 14). (Eastern Asia) . . . . *Neohapalothrix* Kitakami
Antennae 13- or 14-segmented; claws toothed or thickened at base. . . . . (*Dimorphotarsa* Lutz) 17

17. Males with last tarsal segment short and with a conspicuous hairy protuberance (epicondyle) at base; females with the segment longer and without this enlargement. (Southern South America) . . . . Subgen. *Dimorphotarsa* Lutz

    Last tarsal segment simple in both sexes. (Southern South America) . . . . Subgen. *Metacurupira*, nom. nov. (for *Curupira*, preoccupied)

18. Antennae 9-segmented; *Rs* with a single branch; Anal vein lacking (Fig. 18 (Central Asia) . . . . *Tianschanella* Brodsky

    Antennae 13- to 15-segmented; *Rs* forked near outer end into R_4 and R_5; Anal vein represented by at least a short basal spur (Figs. 13, 16, 17) 19

19. Body clothed with abundant long erect setae; antennae 13-segmented; Anal vein reaching wing margin (Fig. 16). (Central Europe) . . . . *Hapalothrix* Loew

    Body nearly glabrous; antennae 15-segmented; Anal vein not reaching the wing margin (Figs. 13, 17) 20

20. Tibial spurs present; posterior basitarsus unmodified; Anal lobe of wing moderately developed (Fig. 13). (Neotropical) . . . . *Paltostoma* Schiner

    Tibial spurs lacking; posterior basitarsus enlarged; Anal lobe of wing large and conspicuous (Fig. 17). (Neotropical) . . . . *Limonicola* Lutz

21. A single radial vein preserved, *Rs* and branches atrophied (Fig. 23). (Ceylon; south India) . . . . *Hammatorrhina* Loew

    Two or three radial veins reach the wing margin, *Rs* preserved (Figs. 19–22) . . . 22

22. *Rs* forked at outer end into two branches, R_4 and R_5 (Fig. 19) (*Neocurupira* Lamb) 23

    Rs with a single branch (Figs. 20–22) 24

23. Eyes holoptic in male, dichoptic in female; Anal angle of wing very prominent.. (New Zealand; southeastern Australia) . . . . Subgen. *Neocurupira* Lamb

    Eyes dichoptic in both sexes; Anal angle of wing obtuse and inconspicuous. (New Zealand . . . . Subgen. *Paracurupira* Tillyard

24. *Rs* very short to almost lacking, appearing as a transverse vein that is shorter than *r-m* which is in longitudinal alignment with the branch of *Rs*, the latter sinuous, at margin ending close to R_{1+2+3}, greatly narrowing cell R_3; wings of female commonly patterned with darker at tip (Fig. 22). (Southern Europe; southern and eastern Asia; eastern Australia) . . . . *Apistomyia* Bigot

    Rs longer, approximately one-half as long as the subtransverse *r-m*; branch of *Rs* straight, diverging from R_{1+2+3}, cell R_3 at margin nearly as extensive as cell R_5; wings unpatterned (Figs. 20, 21) 25

25. Antennae 11- or 12-segmented; males with eyes dichoptic, not divided by a bare strip; Anal vein entire, reaching the margin (Fig. 20) New Zealand) . . *Peritheates* Lamb

    Antennae 8- or 9-segmented; males with eyes holoptic, bisected by a bare strip; Anal vein not reaching the margin (Fig. 21). (North India: Himalayas) . . . . *Horaia* Tonnoir

THE GENERA AND SPECIES OF BLEPHAROCERIDAE

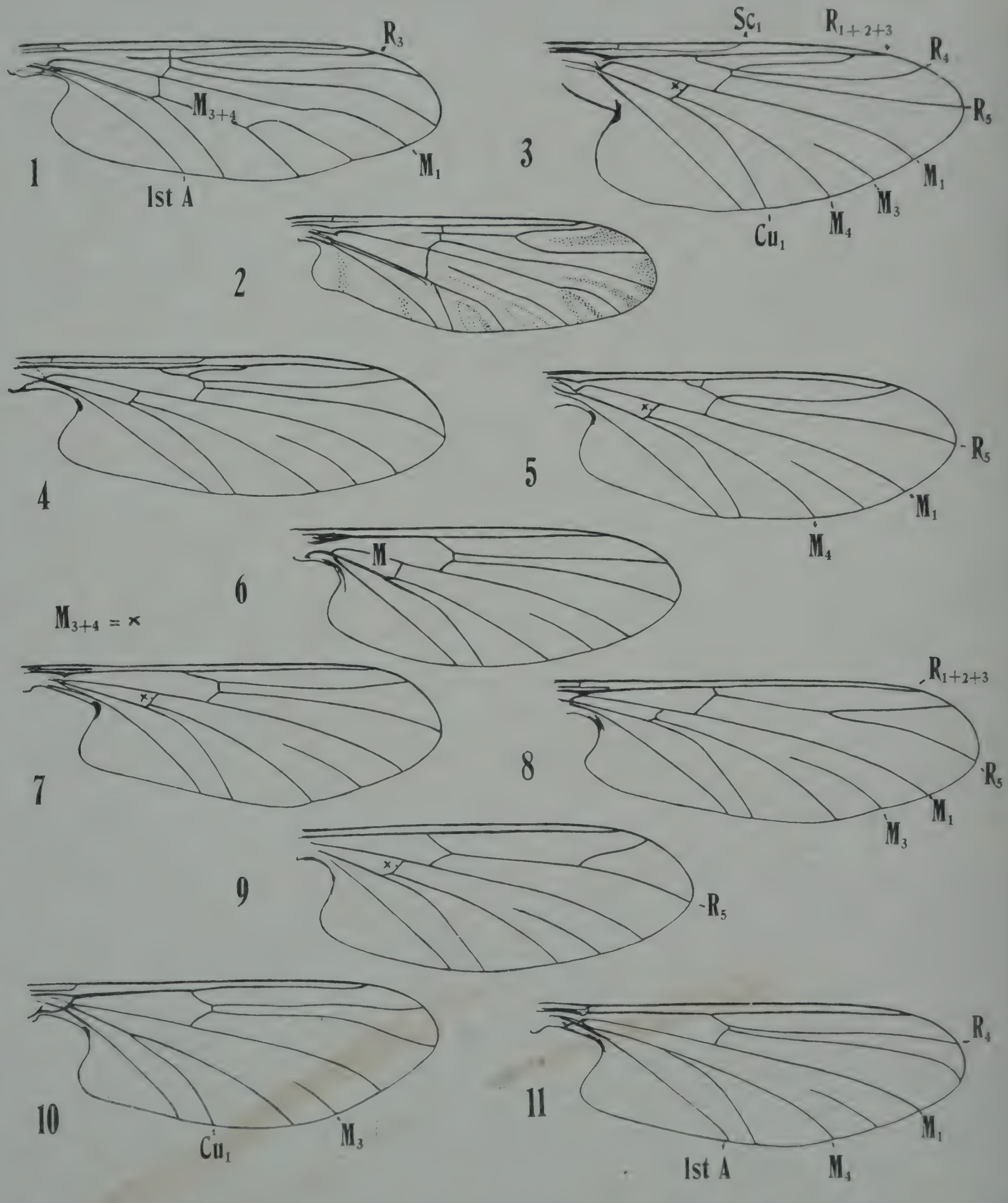
The number of valid species remains in question since several are insufficiently known and some may fall in the synonymy. The species of *Dimorphotarsa* described by Lutz (1920) were based primarily on the larva and pupa, and the adults of certain of these remain undiscovered. References to subspecies in *Liponeura* are omitted (for such, consult Mannheims, 1935, 1937, 1954). The lists of genera and species are arranged alphabetically.

Agathon von Röder

Agathon von Röder; Wien. Entomol. Zeitg. 9: 230; 1890. (Type, *elegantula* von Röder).

Included species: (*bilobatoides* Kitakami, 1931, as *Philorus*. See *Dioptopsis*); (*canadensis* Garrett, 1922, as *Bibiocephala*. See *comstocki*); *comstocki* (Kellogg, 1903, as *Bibiocephala*) Western U.S. and Canada; *doanei* (Kellogg, 1900, as *Liponeura*) Western U.S.; *elegantula* von Röder, 1890, Western U.S. and Canada; *iyaensis* (Kitakami, 1931, as *Bibiocephala*) Japan; *japonica* (Alexander, 1922, as *Bibiocephala*) Japan; *kawamurai kawamurai* (Kitakami, 1950, as *Bibiocephala*) North Korea; *kawamurai ezoensis* (Kitakami, 1950, as *Bibiocephala*) Karafuto, Japan; (*longispina* Kitakami, 1931, as *Philorus*. See *Dioptopsis*); *montana montana* (Kitakami, 1931, as *Bibiocephala*) Japan; *montana bispina* (Kitakami, 1931, as *Bibiocephala*) Japan.

Virtually all species were originally described in *Bibiocephala*. The genus *Dioptopsis* seems to be merely a further modification of the present group in which vein R_3 has been lost by recession into the axil of *Rs*, as was discussed under venation in the Introduction.

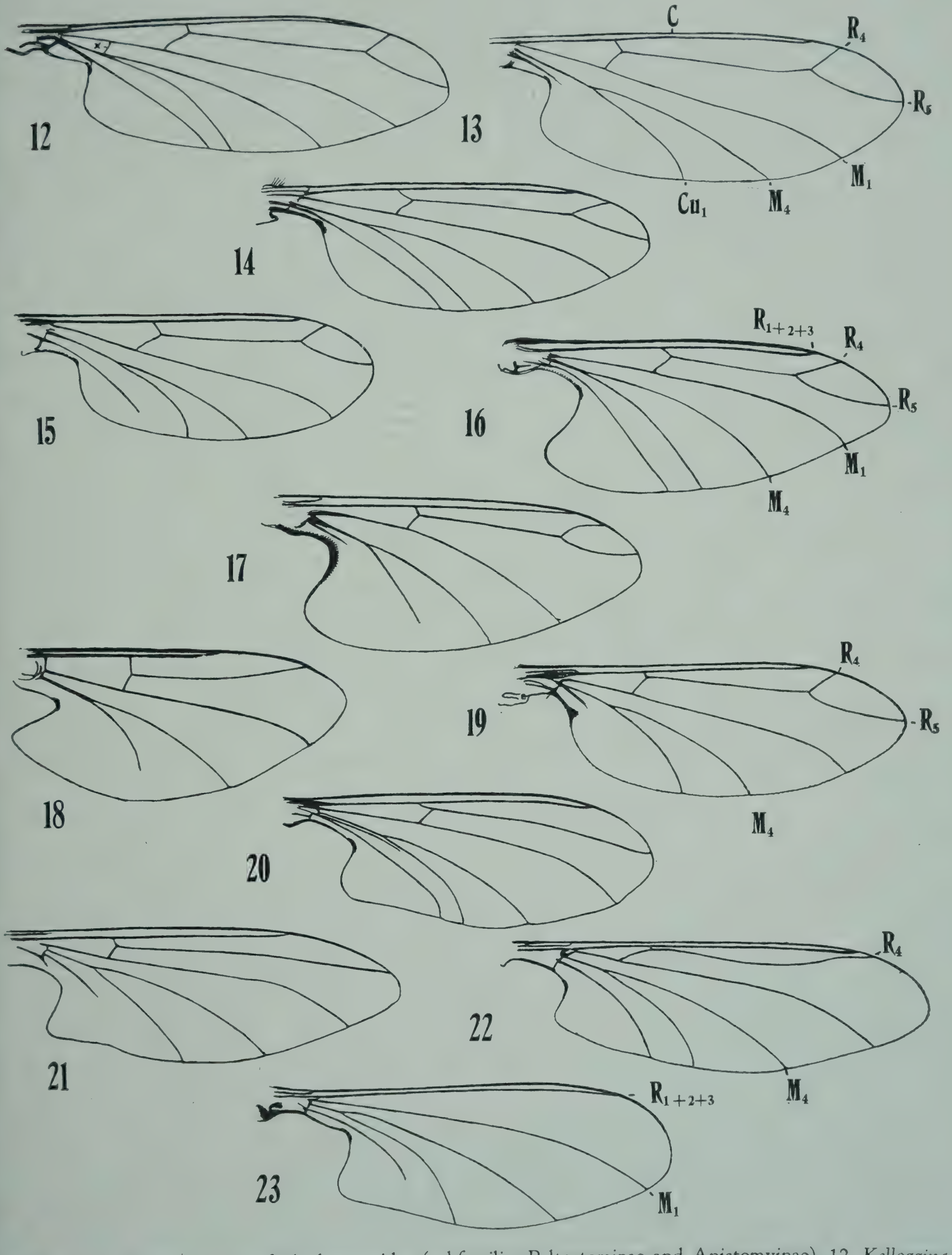


Figs. 1–11. Wing venation of Blepharoceridae (subfamilies Edwardsininae and Blepharocerinae). 1, *Edwardsina chilensis* Alexander; 2, *Paulianina hova* Alexander; 3, *Bibiocephala grandis* Osten Sacken; 4, *Agathon comstocki* (Kellogg); 5, *Agathon doanei* (Kellogg); 6, *Dioptopsis sequoiarum* (Alexander); 7, *Dioptopsis djordjevici* (Komárek); after Komárek; 8, *Philorus yosemite* (Osten Sacken); 9, *Philorus horai* (Tonnoir); after Tonnoir; 10, *Blepharocera fasciata* (Westwood); 11, *Liponeura brevirostris* Loew.

Apistomyia Bigot

Apistomyia Bigot; Ann. Soc. Entomol. France (4) 2: 109; 1862. (Type, *elegans* Bigot).

Included species: *collini* Bezzi, 1913, Queensland; *elegans* Bigot, 1862, Southern Europe; *mackerrasi* Tonnoir, 1930, Java; *maior* Bischoff, 1932, Java; *minor* Bischoff, 1932, Java; *nigra* Kitakami, 1941, Formosa; *tonnoiri* Tillyard, 1922, New South Wales; *trilineata* Brunetti, 1911, North India; *uenoi* (Kitakami, 1931, as *Curupira*) Japan.



Figs. 12–23. Wing venation of Blepharoceridae (subfamilies Paltostominae and Apistomyinae). 12, *Kelloggina rufescens* (Williston); 13, *Paltostoma delectata* Alexander; 14, *Neohapalothrix kanii* Kitakami; 15, *Elporia capensis* Edwards; 16, *Hapalothrix lugubris* Loew; 17, *Limonicola plurivectis* Lutz; after Lutz; 18, *Tianschanella monstruosa* Brodsky; after Brodsky; 19, *Neocurupira hudsoni* Lamb; 20, *Peritheates turrifer* Lamb; 21, *Horaia montana* Tonnoir; 22, *Apistomyia elegans* Bigot; 23, *Hammatorrhina bella* Loew.

Bibiocephala Osten Sacken

Bibiocephala Osten Sacken; Ann. Rept. U.S. Geol. & geog. Surv. Terr. 1873: 564; 1874. (Type, *grandis* Osten Sacken).

Bibionus Curran; Canad. Ent. 55: 266–269; 1923. (Type, *griseus* Curran).

Amika Kitakami; Jour. Kumamoto Women's Univ. 2: 37–39; 1950. (Type, *infuscata* Matsumura).

Included species: *grandis* Osten Sacken, 1874, Western North America; *griseus* (Curran, 1923, as *Bibionus*) Western Canada; *infuscata infuscata* (Matsumura, 1916, as *Liponeura*) Japan; *infuscata minor* Kitakami, 1931, Japan; *kelloggi* Garrett, 1922, Western Canada; *komaensis* (Kitakami, 1950, as *Amika*) S. Manchuria, North Korea.

The following species described in *Bibiocephala* are now placed in *Agathon*: *comstocki*, *iyaensis*, *japonica*, *kawamurai* and *montana*. Matsumura (*In* 6000 Illustrated Insects of Japan-Empire, p. 407, fig.; 1931) describes as a *Liponeura* a species that he names *jezoensis* that is evidently a member of this genus. It may be a pale form of *infuscata* or possibly may refer to *komaensis*, which still is known only from the immature stages.

Blepharocera Macquart

Blepharicera Macquart; Ann. Soc. Entomol. France (2) 1: 61; 1843. (Type, *fasciata* Westwood, as *limbipennis* Macquart). Emended to *Blepharocera* Agassiz, 1846.

Asthenia Westwood; Magazin de Zoologia (2) 4, pl. 94; 1842. (Type, *fasciata* Westwood). Preoccupied by *Asthenia* Hübner, 1825; *Asthenia* Westwood, 1841 (Lepidoptera).

Subgenus *Blepharocera* Macquart

Included species: *apoensis* Alexander, 1952, Mindanao; *armeniaca* Komárek, 1914, Armenia; *capitata* (Loew, 1863, as *Blepharoptera*, lapsus) Eastern U.S.; *dimorphops* Alexander, 1953, Eastern China; *fasciata fasciata* (Westwood, 1842, as *Asthenia*) Europe; *fasciata asiatica* Brodsky, 1930, Central Asia; *indica* Brunetti, 1911, North India; *japonica* Kitakami, 1931, Japan; *jordani* Kellogg, 1903, Western U.S.; *kuenlunensis* Lackschewitz, 1935 (*limbipennis* Macquart, 1843. See *fasciata*) Central Asia; *osten-sackeni* Kellogg, 1903, Western U.S.; *similans* Johannsen, 1929, Eastern U.S.; *taiwanica* Kitakami, 1937, Formosa; *tenuipes* (Walker, 1848, as *Asindulum*) Northern N. America; *tetrophthalma* Edwards, 1933, Borneo; *thurmanae* Alexander, 1953, Thailand; *uenoi* Kitakami, 1937, Formosa; *williamsae* Alexander, 1953, Eastern U.S.; *yamasakii* Kitakami, 1950, Manchuria; *yankovskyi* Alexander, 1953, North Korea; *zionensis* Alexander, 1953, Southwestern U.S.

Subgenus *Parablepharocera* Kitakami

Parablepharocera Kitakami; Mem. Coll. Sci., Kyoto Imper. Univ., (B) 6, no. 2, art. 4: 97; 1931. (Type, *esakii* Alexander).

Included species: *esakii* Alexander, 1924, Japan; *shirakii* Alexander, 1922, Japan.

Dimorphotarsa Lutz

Dimorphotarsa Lutz; Mem. Inst. Oswaldo Cruz 12, fasc. 1: 29–30; 1920. (Type, *fascibranchia* Lutz).

Dimorphotaenia Lutz; Mem. Inst. Oswaldo Cruz 12, fasc. 1: 26; 1920. (Type, *bocainae* Lutz). Lapsus for *Dimorphotarsa*.

Curupira Osten Sacken; Berlin. Entomol. Zeitschr. 40: 162; 1895. (Type, *torrentium* Müller). Preoccupied by *Curupira* Distant, 1888 (Hemiptera).

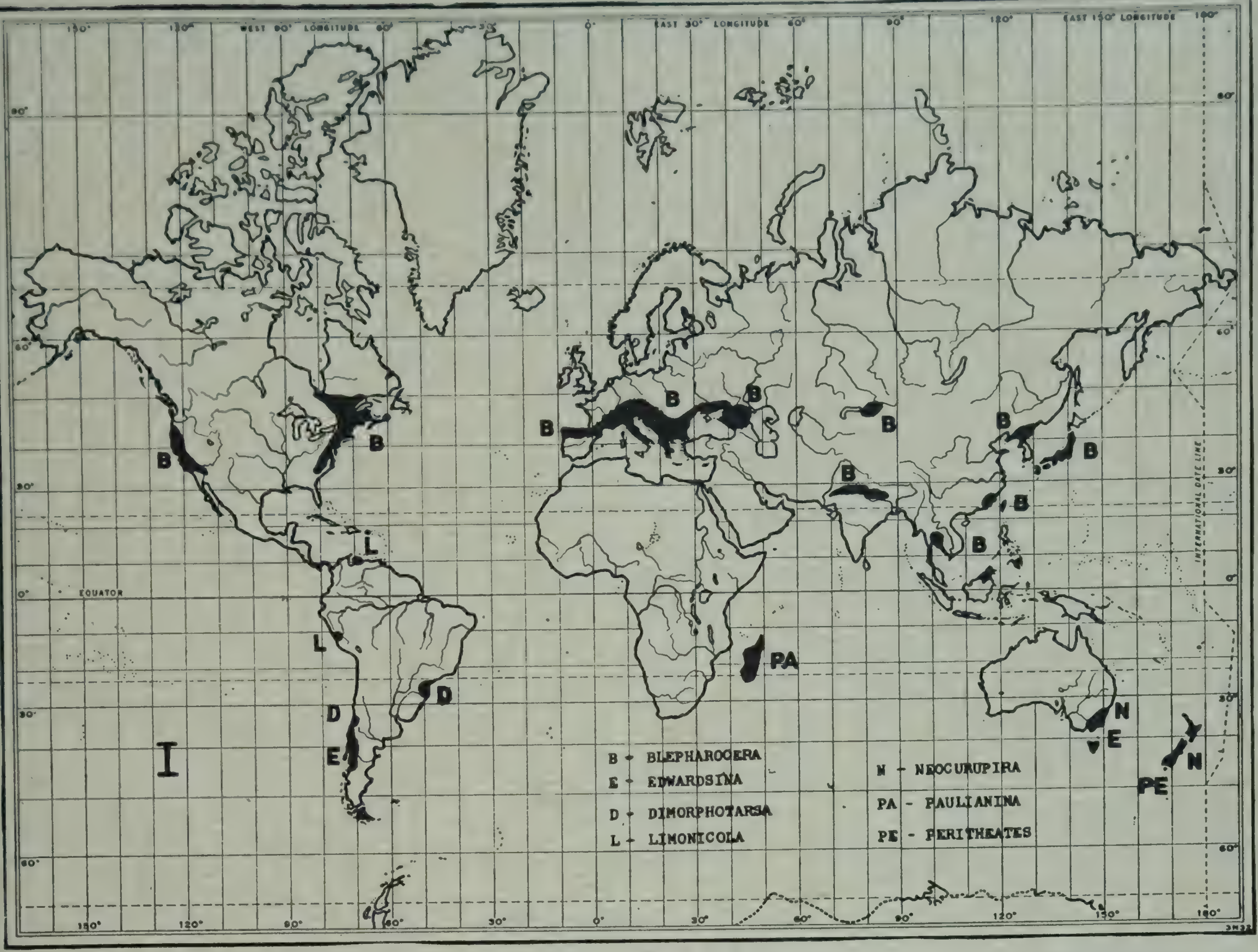
Subgenus *Dimorphotarsa* Lutz

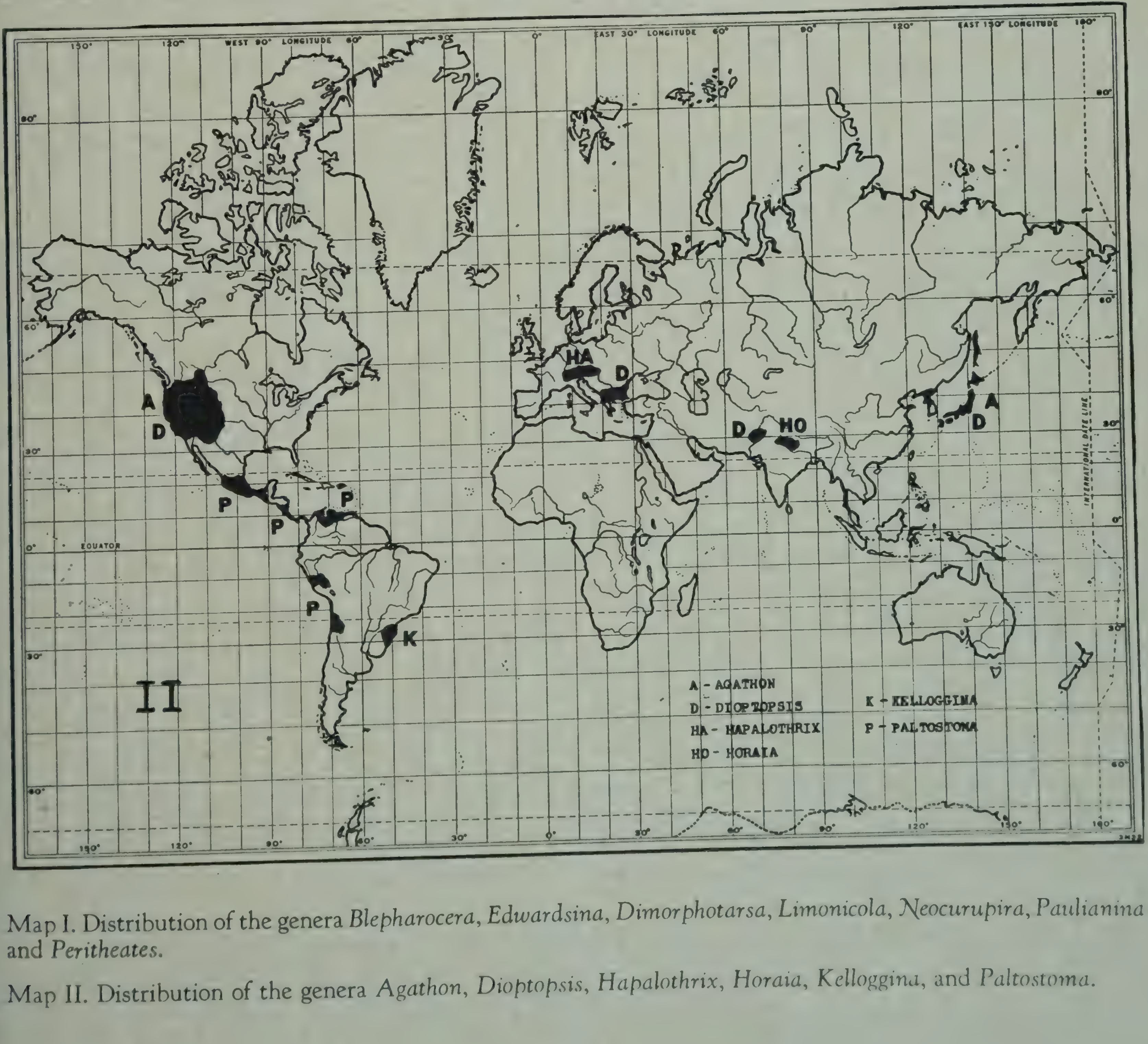
Included species: *bocainae* Lutz, 1920 (as *Dimorphotaenia*, lapsus), SE Brazil; *brevicornis* (Edwards, 1929, as *Curupira*) NE Argentina; *fascibranchia* Lutz, 1920, SE Brazil; *lorenzi* Lutz, 1920, SE Brazil; *tetragoneura* Lutz, 1920, SE Brazil; *tetrasticha* Lutz, 1920, SE Brazil.

Subgenus *Metacurupira* novum

(renaming of *Curupira* Osten Sacken, preoccupied).

Included species: *brevivectis* (Lutz, 1920, as *Curupira*) SE Brazil; *chilena* (Alexander. 1952, as *Curupira*) C. Chile; *disticha* (Lutz, 1920, as *Curupira*) SE Brazil; *garciana* (Lutz, 1920, as *Curupira*) SE Brazil; *granulipupa* (Lutz, 1920, as *Curupira*) SE Brazil; *hirtipupa* (Lutz, 1920, as *Curupira*) SE Brazil; *horrens* (Lutz, 1920, as *Curupira*) SE Brazil; *incerta* (Lutz, 1920, as *Curupira*) SE Brazil; *mochlura* (Lutz, 1920, as *Curupira*) SE Brazil; *muelleri* (Lutz, 1920, as *Curupira*) SE Brazil; *pluripunctata* (Lutz, 1920, as *Curupira*) SE Brazil; *spinivectis* (Lutz, 1920, as *Curupira*) SE Brazil; *torrentium* (Müller, 1880, as *Paltostoma*) SE Brazil.


I
B - BLEPHAROCERA
E - EDWARDSINA
D - DIMORPHOTARSA
L - LIMONICOLA
N - NEOCURUPIRA
PA - PAULIANINA
PE - PERITHEATES
WEST 90° LONGITUDE
EAST 30° LONGITUDE
EAST 150° LONGITUDE
EQUATOR
INTERNATIONAL DATE LINE


II
A - AGATHON
D - DIOPTOPSIS
HA - HAPALOTHRIX
HO - HORAIA
K - KELLOGGINA
P - PALTOSTOMA
WEST 90° LONGITUDE
EAST 30° LONGITUDE
EAST 150° LONGITUDE
EQUATOR
INTERNATIONAL DATE LINE

Map I. Distribution of the genera *Blepharocera, Edwardsina, Dimorphotarsa, Limonicola, Neocurupira, Paulianina* and *Peritheates.*

Map II. Distribution of the genera *Agathon, Dioptopsis, Hapalothrix, Horaia, Kelloggina,* and *Paltostoma.*

Dioptopsis Enderlein

Dioptopsis Enderlein, Mitth. deutsch. Ent. gesell., 7: 43. Zweiflügler, Diptera. Tierwelt Mitteleur. 6, Teil III, Lief. 2: 8; 1936. (Type, *djordjevici* Komárek).

Included species: *aylmeri* (Garrett, 1923, as *Philorus*) Western Canada; *bilobatoides* (Kitakami, 1931, as *Philorus*) Japan; *bionis* (Agharkar, 1914, as *Philorus*) Kashmir; *cheaini* (Garrett, 1925, as *Philorus*) Western Canada; *djordjevici* (Komárek, 1931, as *Philorus*) SE. Europe; *longispina* (Kitakami, 1931, as *Philorus*) Japan; *markii* (Garrett, 1925, as *Philorus*) Western No. America; *sequoiarum* (Alexander, 1952, as *Philorus*) Western U.S.; *tianschanica tianschanica* (Brodsky, 1930, as *Philorus*) Central Asia; *tianschanica nivium* (Brodsky, 1937, as *Philorus*) Central Asia.

From its venation, *Dioptopsis* evidently represents a reduction from *Agathon* where the short element R_3 is lost by basal recession into the axil of *Rs*. Kitakami (1950) had placed his two species, *bilobatoides* and *longispina* in *Agathon* (as *Bibiocephala*). *Liponeura bilobata* Loew, 1869, evidently is a true *Liponeura* but had been referred to the present group by various writers, as Kellogg, Kitakami and Tonnoir, on the basis of preservation of the basal section of vein M_{3+4} in some specimens. Tonnoir (1931) suggests that *tianschanica* may be a synonym of the earlier described *bionis* Agharkar.

Edwardsina Alexander

Edwardsina Alexander; Arkiv för Zoologi 13, no. 7: 2–3; 1920. (Type, *chilensis* Alexander).

Subgenus *Edwardsina* Alexander

Included species: *argentinensis* Alexander, 1922, S. Argentina; *chilensis* Alexander, 1920, S. Chile; *chilota* Edwards, 1929, S. Chile; *dentulosa* Edwards, 1934, S. Chile; *dispar* Edwards, 1929, S. Chile; *fuscipes* Edwards, 1929, S. Chile; *luteipleura* Alexander, 1953, S. Chile; *stigmatica* Edwards, 1929, S. Chile.

Subgenus *Alexina* Edwards

Alexina Edwards; Diptera Patagonia & S. Chile 2, fasc. 2: 45; 1929. (Type, *australiensis* Tillyard).

Included species: *australiensis* Tillyard, 1922, SE Australia; (unnamed species, Mannheims, 1938: 330–331) S. Chile.

Subgenus *Tonnoirina* Edwards

Tonnoirina Edwards; Diptera Patagonia & S. Chile 2, fasc. 2: 56; 1929. (Type, *tasmaniensis* Tonnoir).

Included species: *confinis* Tonnoir, 1924, Tasmania; *ferruginea* Tonnoir, 1924, Tasmania; *fluviatilis* Tonnoir, 1924, Tasmania; *gracilis* Edwards, 1929, S. Chile; *montana* Tonnoir, 1924, Tasmania; *nigra* Edwards, 1929, S. Chile; *similis* Tonnoir, 1924, Tasmania; *tasmaniensis* Tonnoir, 1924, Tasmania; *tillyardi* Tonnoir, 1923, SE Australia.

Elporia Edwards

Elporia Edwards; Ann. Mag. Nat. Hist. (8) 16: 203–205; 1915. (Type, *barnardi* Edwards).

Included species: *anisonyx* Barnard, 1947, S. Africa; *armata* Stuckenberg, 1955, S. Africa; *barnardi* (Edwards, 1912, as *Kelloggina*) S. Africa; *capensis* Edwards, 1915, S. Africa; *capra* Barnard, 1947, S. Africa; *edwardsi* Stuckenberg, 1955, S. Africa; *elnorae* (Edwards, 1929, as *Curupira*, *Elporia*) Argentina; *femoralis* Stuckenberg, 1955, S. Africa; *flavopicta* (Edwards, 1932, as *Curupira*) S. Africa; *hiemis* Stuckenberg, 1955, S. Africa; *hystrix* (Edwards, 1933, as *Curupira*) S. Africa; *natalensis natalensis* Stuckenberg, 1955, S. Africa; *natalensis oliffi* Stuckenberg, 1955, S. Africa; *saltatrix* Stuckenberg, 1955, S. Africa; *scruposa* Stuckenberg, 1955, S. Africa; *spinulosa* Edwards, 1916, S. Africa; *uniradius* Barnard, 1947, S. Africa; *vidua* Stuckenberg, 1955, S. Africa.

I am following Stuckenberg (1955) in maintaining this as distinct from *Dimorphotarsa* Lutz (*Curupira*, olim). However, the two groups are very closely related and *Elporia*, *Dimorphotarsa*, and *Metacurupira* may finally be placed as subgenera under the oldest generic name, which is *Elporia*.

Hammatorrhina Loew

Hammatorrhina Loew; Bull. Soc. Entomol. Ital. 1: 94; 1869. (Type, *bella* Loew).

Included species: *bella* Loew, 1869, Ceylon; *pulchra* Edwards, 1927, Ceylon.

Edwards has indicated that the genus is also found in South India.

Hapalothrix Loew

Hapalothrix Loew; Deutsche Entomol. Zeitschr. 20: 211; 1876. (Type, *lugubris* Loew).

Included species: *lugubris* Loew, 1876, Europe.

Horaia Tonnoir

Horaia Tonnoir; Rec. Indian Mus. 32: 193–199, 209–210; 1930. (Type, *montana* Tonnoir).

Included species: *longipes* Tonnoir, 1932, N. India; *montana* Tonnoir, 1930, Assam.

Kelloggina Williston

Snowia Williston; Kansas Univ. Quart. 1: 120; 1893. (Type, *rufescens* Williston). Preoccupied by *Snowia* Neumogen, 1884.

Sackeniella Williston; Trans. Ent. Soc. London 1896: 270; 1896. (Renaming of *Snowia*; preoccupied by *Sackeniella* Meunier, 1895).

Kelloggina Williston; Journ. N.Y. Ent. Soc. 15: 1; 1907. (Renaming of *Snowia*, *Sackeniella*).

Included species: *rufescens* (Williston, 1893, as *Snowia*) SE Brazil.

Limonicola Lutz

Limonicola Lutz; Estudios de zoologia y parasitologia Venezolanas p. 67, 2 pls.; 1928. (Type, *plurivectis* Lutz).

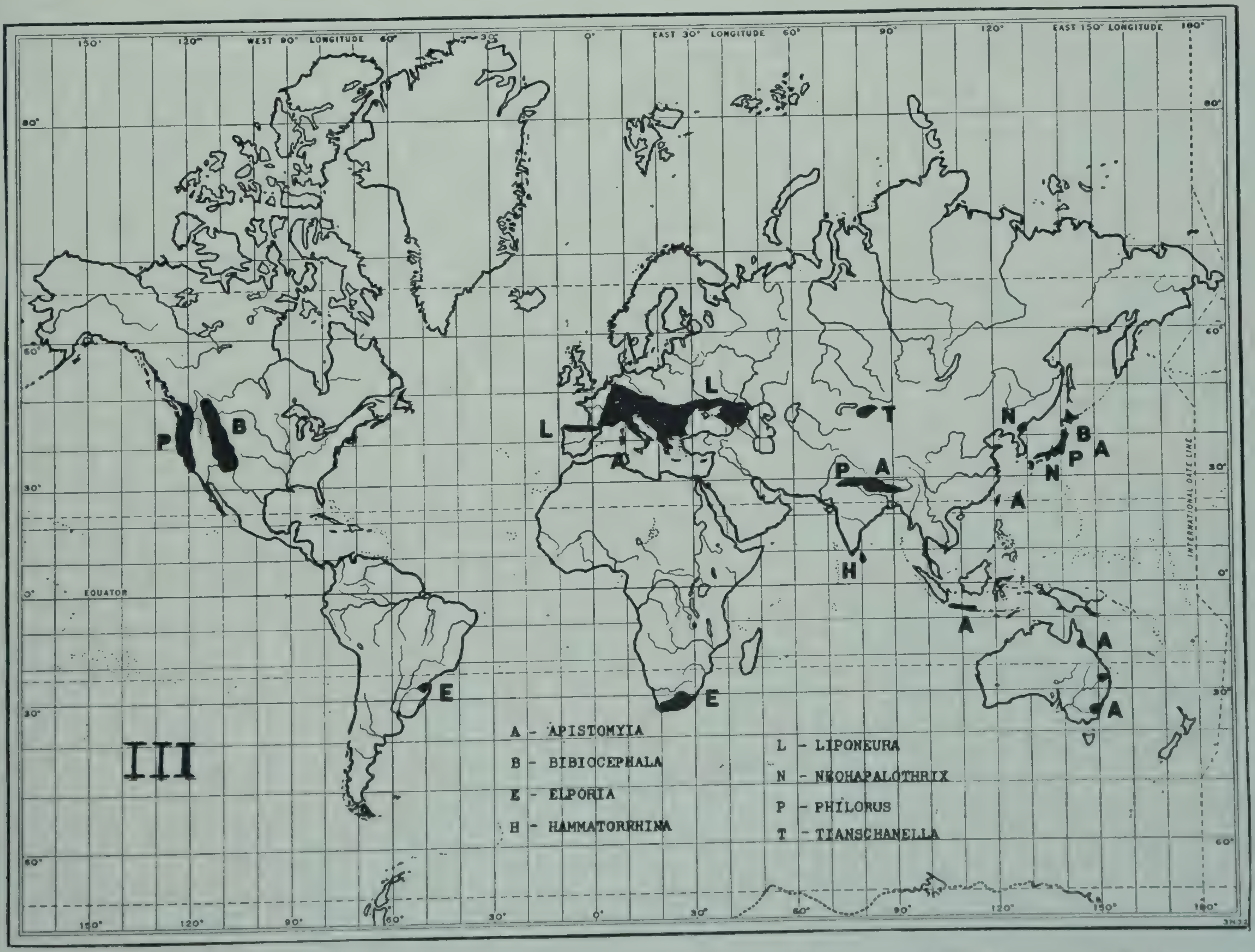
Included species: *leucoptera* Edwards, 1929, Peru; *plurivectis* Lutz, 1928, Venezuela.

Liponeura Loew

Liponeura Loew; Stettin. Entomol. Zeitg. 5: 118; 1844. (Type, *cinerascens* Loew).

Cardiocrepis Enderlein; Zweiflügler, Diptera. Tierwelt Mitteleur. 6, Teil III, Lief. 2, 16: 8; 1936. (Type, *brevirostris* Loew).

Included species: (*belgica* Bischoff, 1924, = *decipiens*) *bilobata* Loew, 1869, Europe; *bischoffi* Edwards, 1928, Europe; *brevirostris* Loew, 1877, Europe; *buresi* Komàrek & Vimmer, 1934, Europe; *cinerascens* Loew, 1844, Europe; *cordata* Vimmer, 1916, Europe; *decipiens* Bezzi, 1912, Europe; *edwardsiana* Mannheims, 1954, Europe; *euryfrons* Bischoff, 1935, Caucasus; (*klapaleki* Komárek, 1931, = *buresi*) (*klapaleki* Vimmer, 1916, = *komareki*) *komareki* Vimmer, 1916, Europe; *minor* Bischoff, 1922, Europe; *platyfrons* Komárek, 1914,


III
A - APISTOMYIA
B - BIBIOCEPHALA
E - ELPORIA
H - HAMMATORRHINA
L - LIPONEURA
N - NEOHAPALOTHRIX
P - PHILORUS
T - TIANSCHANELLA
EQUATOR
INTERNATIONAL DATE LINE
WEST 90° LONGITUDE
EAST 30° LONGITUDE
EAST 150° LONGITUDE

Map III. distribution of the genera *Apistomyia*, *Bibiocephala*, *Elporia*, *Hammatorrhina*, *Liponeura*, *Neohapalothrix*, *Philorus*, and *Tianschanella*.

Caucasus; *tarnogradskyi* Bischoff, 1930, Caucasus; *thienemanni* Bischoff, 1930, Caucasus; *vimmeri* Mannheims, 1954, Europe; (*vogesiaca* Hubault, 1927, = *brevirostris*).

For detailed synonymy and races, consult Mannheims (1935, 1937, 1954). In *bilobata*, some specimens have retained the basal section of vein M_{3+4}, as in *Dioptopsis*; various authors, including Kellogg, Kitakami and Tonnoir, have referred the species to *Philorus* but it evidently is correctly assigned to *Liponeura*.

Neocurupira Lamb

Neocurupira Lamb; Trans. N.Z. Inst. 45: 72–73, figs; 1913. (Type, *hudsoni* Lamb).

Subgenus *Neocurupira* Lamb

Included species: *hudsoni* Lamb, 1913, New Zealand; *nicholsoni* Tillyard, 1922, SE Australia.

Subgenus *Paracurupira* Tillyard

Paracurupira Tillyard; N.Z. Journ. Sci. & Tech. 5: 104–105, figs.; 1922. (Type, *chiltoni* Campbell).

Included species: *chiltoni* (Campbell, 1921, as *Curupira*) New Zealand.

Neohapalothrix Kitakami

Neohapalothrix Kitakami; Mem. Coll. Sci., Kyoto Imper. Univ., (B) 14: 341–344; 1938. (Type, *kanii* Kitakami).

Included species: *kanii* Kitakami, 1938, Japan; *manschukuensis* (Mannheims, 1938, as *Curupira*) Manchuria.

Paltostoma Schiner

Paltostoma Schiner; Verh. zool.-bot. Ges. Wien 16: 931; 1866. (Type, *superbiens* Schiner).

Included species: *argyrocincta* Curran, 1927, Puerto Rico; *bellardii* Bezzi, 1913, Mexico; *delectata* Alexander, 1953, Costa Rica; *lobata* Edwards, 1929, Peru; *parviceps* Alexander, 1953, Peru; *saltana* Edwards, 1929, N. Argentina; *schineri* Williston, 1896, Lesser Antilles; *shannoni* Edwards, 1929, Peru; *superbiens* Schiner, 1868, C. & N. So. America.

Paulianina Alexander

Paulianina Alexander; Mem. Inst. Scient. Madagascar (E) 1: 227–230; 1952. (Type, *hova* Alexander).

Included species: *hova* Alexander, 1952, Madagascar; *robinsoni* Alexander, 1956, Madagascar.

The discovery within very recent years of a primitive genus of Blepharoceridae in Madagascar was one of the surprising additions to our knowledge of the family. Even before the genus was described, Dr. Renaud Paulian had done considerable work on the fresh water fauna and had found no fewer than eight distinct types of larvae, none associated with the adults (Paulian, 1953). In 1956, entomologists from the Natal Museum visited Madagascar and the Dipterologist, Mr. Brian Stuckenberg, made further striking discoveries that make it appear certain that we here are dealing with a genus with many species in the island. At my request, Mr. Stuckenberg prepared the following statement: "In Madagascar I got material of seven species: larvae, pupae and many adults of three species; larvae and mature pupae from which adults can be dissected of two species; and larvae only of two species. These were obtained from two localities, Perinet and the Ankaratra Massif. Paulian had not found Blepharocerids at those places and I believe that all the species which I have are new. The total number of species in Madagascar must be very large: 1. The eight larval types described by Paulian evidently represent undescribed adults; that gives a minimum of 17 species $(2+7+8=17)$. 2. Isolation is an important factor in speciation in this family, and there are very many suitable, isolated places in Madagascar which have not yet been explored for these flies. 3. The localities where they have been found have not been properly collected—I am sure that several species probably occur in each suitable habitat, e.g., at Perinet I found, after systematic collecting, four species in one waterfall. 4. The possibility of a limited seasonal distribution has not yet been investigated, and there may be short-lived species that can only be found during one or other of the seasons, as in South Africa. I am not sure about the occurrence of other genera in Madagascar. The larva described by Paulian as belonging to the Apistomyinae seems to represent such a genus, but I do not think it is *Elporia* as the larva is evidently different from those of the South African species, of which I have seen all the described forms. I have started work on the morphology of the adult flies and what I have found so far confirms that *Paulianina* is very closely related to *Edwardsina*. The nature of the head and mouthparts is virtually identical. The pupae seem to show several different types of respiratory apparatus, not unlike some of those found in *Edwardsina*. I feel that this may prove a fruitful source of investigation"—Brian R. Stuckenberg.

Peritheates Lamb

Peritheates Lamb; Trans. N.Z. Inst. 45: 74–75, figs.; 1913. (Type, *turrifer* Lamb).

Included species: *harrisi* (Campbell, 1921, as *Apistomyia*) New Zealand; *intermedius* Tillyard, 1922, New Zealand; *turrifer* Lamb, 1913, New Zealand.

Philorus Kellogg

Philorus Kellogg; Proc. California Acad. Sci. (3) Zool. 3: 199; 1903. (Type, *yosemite* Osten Sacken; designated by Coquillett, 1910; Mannheims, 1937).

Euliponeura Tonnoir; Rec. Indian Mus. 32: 176–180, 207, figs.; 1930. (Type, *horai* Tonnoir).

Pelmia Enderlein; Mitth. deutsch. Ent. Gesell. 7: 42; 1936. (Type, *yosemite* Osten Sacken).

Included species: *alpinus* Kitakami, 1931, Japan; *ancilla* (Osten Sacken, 1878, as *Blepharocera*) Western U.S.; *assamensis* (Tonnoir, 1930, as *Euliponeura*) Assam; *chosensis* Kitakami, 1931, Korea; *ezoensis* Kitakami, 1931, Japan; *gokaensis* Kitakami, 1950, Japan; *horai* (Tonnoir, 1930, as *Euliponeura*) N. India; *kibunensis* Kitakami, 1931, Japan; *kongoensis* Kitakami, 1950, Korea; *kuyaensis* Kitakami, 1931, Japan; *longirostris longirostris* Kitakami, 1931, Japan; *longirostris minor* Kitakami, 1931, Japan; *sikokuensis* Kitakami, 1931, Japan; *simasimensis* Kitakami, 1931, Japan; *taiwanensis* Kitakami, 1937, Formosa; *vividus* Kitakami, 1931, Japan; *yosemite* (Osten Sacken, 1877, as *Blepharocera*) Western U.S.

Tianschanella Brodsky

Tianschanella Brodsky; Zool. Anzeig. 90: 137–145, figs.; 1930. (Type, *monstruosa* Brodsky).

Included species: *monstruosa* Brodsky, 1930, Central Asia (Tianshan).

SUMMARY OF DISTRIBUTION OF GENERA

Edwardsininae—Restricted to Southern Hemisphere.

Blepharocerinae—Restricted to Northern Hemisphere.

Paltostominae—Both Hemispheres: Old World, 4; New World, 5.

Apistomyinae—Both Hemispheres: Old World, 5; New World, 0.

Nearctic (5 genera): Blepharocerinae—*Agathon*, *Bibiocephala*, *Blepharocera*, *Dioptopsis*, *Philorus*.

Neotropical (6 genera): Edwardsininae—*Edwardsina*. Paltostominae—*Dimorphotarsa*, *Elporia*, *Kelloggina*, *Limonicola*, *Paltostoma*.

Western Palaearctic (Europe) (5 genera): Blepharocerinae—*Blepharocera*, *Dioptopsis*, *Liponeura*. Paltostominae—*Hapalothrix*. Apistomyinae—*Apistomyia*.

Eastern Palaearctic and Oriental (10 genera): Blepharocerinae—*Agathon*, *Bibiocephala*, *Blepharocera*, *Dioptopsis*, *Philorus*. Paltostominae—*Neohapalothrix*, *Tianschanella*. Apistomyinae—*Apistomyia*, *Hammatorrhina*, *Horaia*.

Ethiopian (2 genera): Edwardsininae—*Paulianina*. Paltostominae—*Elporia*.

Australasian (4 genera): Edwardsininae—*Edwardsina*. Apistomyinae—*Apistomyia*, *Neocurupira*, *Peritheates*.

REFERENCES

The following record includes only the more important references to the family. Local lists, descriptions of individual species, short life-histories, and comparable brief articles are omitted. The papers that describe new genera and subgenera are included, regardless of length. Certain of the papers cited include more detailed lists of papers concerning the family and such special bibliographies are noted. Of particular value are the critical summaries of literature provided by Bezzi, 1913 (for the years 1842 through 1912) and 1914 (for the years 1881 through 1913), Hubault, 1927 (1914 through 1925), and Mannheims, 1935 (1927 through 1934).

Outstanding workers on the family include Bezzi, Edwards, Kellogg, Kitakami, Komàrek, Loew, Mannheims, Osten Sacken, Stuckenberg, Tillyard, and Tonnoir. Those who have devoted particular attention to the immature stages, additional to certain of the above, include Bischoff, Brodsky, Campbell, Hetschko, Hofeneder, Müller, Lutz, Paulian, Scott, and Stuckenberg.

Agharkar, S. P. 1914. On a new species of blepharocerid fly from Kashmir, together with a description of some larvae from the same locality. *Rec. Indian Mus.* 10: 159–164, 2 pls.

Alexander, C. P. 1920. A new genus and species of net-winged midge (Blepharoceridae) and an undescribed species of Tanyderidae (Diptera). *Arkiv för Zoologi* 13, no. 7: 1–7, 2 figs. [*Edwardsina*]

Alexander, C. P. 1952. A new genus and species of net-winged midge from Madagascar (Diptera Blepharoceridae). *Mem. Inst. Scient. Madagascar* (E) 1: 227–230, 1 fig. [*Paulianina*]

Barnard, K. H. 1947. The Blepharoceridae (Diptera) of the S.W. Cape. *Journ. Entomol. Soc. South Africa* 10 (1): 3–15, 7 figs.

Bezzi, Mario. 1913 (1912). Blefaroceridi Italiani. *Bull. Soc. Entomol .Italiana* 44: 3–114, 18 figs. [Annotated bibliography, 1842–1912]

Bezzi, Mario. 1914 (1913). Sui Blepharoceridi della Nuova Zelanda. *Bull. Soc. Entomol. Italiana* 45: 115–129. [Annotated bibliography, 1881–1913]

Bigot, J. M. F. 1862. Dipteres nouveaux de la Corse. *Ann. Soc. Entomol. France* (4) 2: 109–114, 1 pl. [*Apistomyia*]

Bischoff, Wilhelm C. M. 1922. Zur Kenntnis der Blepharoceriden. *Zool. Jahrb., Syst.* 46: 61–120, 10 figs., 4 pls. [Bibliography]

Bischoff, Wilhelm C. M. 1928. Die Okologie der paläarctischen Blepharoceridae. *Erg. und Fortschr. d. Zoologie* 7: 209–278, 53 figs.

Bischoff, Wilhelm C. M. 1930. Neues über paläarktische Blepharoceriden. *Zool. Anzeig.* 92: 9–17, 6 figs.

Bischoff, Wilhelm C. M. 1932. Blepharoceridae aus Java. *Arch. für Hydrobiologie, Suppl. Bd.* 11, *Tropische Binnengewasser* 3: 401–446, 33 figs.

Brodsky, Konstantin. 1930. Zur Kenntnis der Wirbellosenfauna der Bergströme Mittelasiens. III. Blepharoceridae I (Imagines). *Zool. Anzeig.* 90: 129–146, 15 figs. [*Tianschanella*].

Campbell, J. W. 1921. Notes on the Blepharoceridae (Diptera) of New Zealand. *Trans. N. Z. Inst.* 53: 258–288, 4 + 150 figs.

Campbell, J. W. 1923. Notes on the Blepharoceridae (Diptera) of New Zealand. *Trans. N. Z. Inst.* 54: 260–264, 29 figs.

Curran, C. H. 1923. Studies in Canadian Diptera. II. The genera of the family Blepharoceridae. *Canad. Ent.* 55: 266–269 [Key to genera; *Bibionus*].

Edwards, F. W. 1915. On *Elporia*, a new genus of blepharocerid flies from South Africa. *Ann. Mag. Nat. Hist.* (8) 16: 203–215, 22 figs. [*Elporia*]

Edwards, F. W. 1927. Some nematocerous Diptera from Ceylon. *Spolia Zeylanica* 14: 117–128, 2 figs.

Edwards, F. W. 1929. Diptera of Patagonia and South Chile, 2, fasc. 2 (Blepharoceridae): 33–75, 3 figs., 4 pls.

Enderlein, G. 1936. Zweiflügler, Diptera Tierwelt Mitteleur., 6, Teil 3, Lief. 2: 1–259, 317 figs. [*Cardiocrepis, Dioptopsis, Pelmia*]

Hetschko, Alfred. 1911. Zur Kenntnis der Biologie und Verbreitung der *Liponeura*-Arten (Dipt.). *Wien. Entomol. Zeitg.* 30: 273–278.

Hetschko, Alfred. 1912. Biologisches über *Apistomyia elegans* Big. (Dipt. Blepharoc.). *Wien. Entomol. Zeitg.* 31: 305–307.

Hetschko, Alfred. 1912. Die Metamorphose von *Liponeura cinerascens* Lw. (Dipt. Blepharoc.). *Wien. Entomol. Zeitg.* 31: 319–325, 5 figs.

Hetschko, Alfred. 1919. Die larve von *Hapalothrix lugubris* Lw. (Dipt. Blepharoc.). *Wien. Entomol. Zeitg.* 37: 201–206, 1 pl.

Hofeneder, Heinrich. 1927. Uber die Larven der Blepharoceriden und ihren merkwurdigen Anheftungsapparat. *Verh. zool.-bot. Ges. Wien* 77: 82–98, 9 figs.

Hora, Sunder Lal. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. *Phil. Trans. Roy. Soc. London* (B) 218: 172–282, 22 figs., 4 pls.

Hubault, Etienne. 1927. Contribution à l'étude des invertébrés torrenticoles. *Bull. biol. France et Belgique* Suppl. 9: 165–187, 297–312, figs. 36–44, 54, 4 pls. [annotated bibliography 1914–1925]

Johannsen, O. A. 1934. Aquatic Diptera. Part 1. Nemocera, exclusive of Chironomidae and Ceratopogonidae. *Cornell Univ. Agr. Expt. Sta. Mem.* 164: 50–54, figs. 201–204, pl. 23.

Kellogg, Vernon L. 1900. Notes on the structure and life-history of *Blepharocera capitata* Loew. *Ent. News* 11: 305–318, 5 figs.

Kellogg, Vernon L. 1903. The net-winged midges (Blepharoceridae) of North America. *Proc. California Acad. Sci.* (3) *Zool.* 3: 187–221, 1 fig., 5 pls.

Kellogg, Vernon L. 1907. Diptera. Fam. Blepharoceridae. *In* Genera Insectorum (*Wytsman*) 56: 1–15, 2 pls.

Kitakami, Sirô. 1931. The Blepharoceridae of Japan. *Mem. Coll. Sci., Kyoto Imper. Univ.* (B) 6, no. 2, art. 4: 53–108, 10 figs., 10 pls. [Bibliography] [*Parablepharocera*]

Kitakami, Sirô. 1937. Supplementary notes on the Blepharoceridae of Japan. *Mem. Coll. Sci., Kyoto Imper. Univ.* (B) 12, no. 2, art. 5: 115–136, 3 pls. [Bibliography]

Kitakami, Sirô. 1938. A new genus and species of Blepharoceridae from Japan. *Mem. Coll. Sci., Kyoto Imper. Univ.* (B) 14, no. 2, art. 15: 341–352, 3 pls. [Bibliography] [*Neohapalothrix*]

Kitakami, Sirô. 1941. On the Blepharoceridae of Formosa, with a note on *Apistomyia uenoi* (Kitakami). *Mem. Coll. Sci., Kyoto Imper. Univ.* (B) 16, no. 1, art. 3: 59–74, 2 figs., 2 pls.

Kitakami, Sirô. 1950. The revision of the Blepharoceridae of Japan and adjacent territories. *Journ. Kumamoto Women's Univ.* 2: 15–80, 3 figs. (with subfigs.), 5 pls. [Bibliography] [*Amika*]

Komárek, Julius. 1914. Uber die Blepharoceriden aus dem Kaukasus und Armenien. *Sitzb. k.k. Böhm. Gesell. Wissensch.*, Prag, no. 10: 1–19, 2 pls.

Komárek, Julius. 1914. Die morphologie und physiologie der haftscheiben der Blepharoceridenlarven. *Sitzb. k.k. Böhm. Gesell. Wissensch.*, Prag, no. 25: 1–28, 10 figs.

Komárek, Julius. 1921. O larvach evropskch druhu celede Blepharoceridae (Dipt.) *Acta Soc. Ent. Cechoslovaniae* 17: 37–52, 7 figs.

Komárek, Julius, and A. Vimmer. 1922. The larvae of the European Blepharoceridae. *Ann. Biol. Lacustre* 11: 63–77, 7 figs.

Komárek, Julius, and A. Vimmer. 1934. Blepharoceridae Balkanicae. *Mitteil, königlich. Naturwiss. Inst.*, Sofia, Bulgarien, 7: 1–35, 11 figs.

Lamb, C. G. 1912. On two blepharocerids from New Zealand. *Trans. N.Z. Inst.* 45: 70–75, 8 figs. [*Neocurupira; Peritheates*]

Lindner, Erwin. 1930. Die Fliegen der palaarktischen Region, 2, 1, Lief. 50, Blepharoceridae und Deuterophlebiidae, pp. 1–37, 37 figs., 2 pls.

Loew, Hermann. 1844. Beschreibung einiger neuen Gattungen der europäischen Dipterenfauna. *Stettin. Entomol. Zeitg.* 5: 114–130, 154–173, 2 pls. [*Liponeura*]

Loew, Hermann. 1862. Diptera of North America. 1: 1–220, 12 figs., 2 pls.

Loew, Hermann. 1869. La famiglia dei Blefaroceridi (Blepharoceridae). *Bull. Soc. entomol. Italiana* 1: 85–98, 2 pls. [*Hammatorrhina*]

Loew, Hermann. 1876. *Eclimus hirtus* und *Hapalothrix lugubris*, zwei neue europäische Dipteren. *Deutsch. Entomol. Zeitschr.* 20: 209–214 [*Hapalothrix*]

Loew, Hermann. 1877. Revision der Blepharoceridae. *Zeitschr. für Entomol.* (Breslau) 6: 54–98, 1 pl.

Lutz, Adolpho. 1920. Dipteros da familia Blepharoceridae, observados no Brazil. *Mem. Inst. Oswaldo Cruz* 12, fasc. 1: 21–43 (Portuguese text), 16–40 (German text), 7 pls. [*Dimorphotarsa*]

Lutz, Adolpho. 1928. Blefaroceridae. *In* "Estudios de Zoologia y Parasitologia Venezolanas," pp. 65–69, 2 pls. [*Limonicola*]

Macquart, J. M. 1843. Description d'un nouveau genre d'insectes diptères. *Ann. Soc. Entomol. France* (2) 1: 59–63, pl. 3. [*Blepharicera*]

Mackerras, I. M., and M. T. Mackerras. 1951. *Apistomyia collini* Bezzi (Diptera, Blepharoceridae) in North Queensland. *Proc. Roy. Soc. Queensland* 52: 29–32, 1 pl.

Mannheims, B. J. 1935. Beiträge zur biologie und morphologie der Blepharoceriden (Dipt.). *Zoologische Forschungen*, Leipzig, 2: 1–115, 95 figs. [Annotated bibliography, 1927–1934]

Mannheims, B. J. 1937. Zur synonymie der europaischen Blepharoceriden (Dipt.). *Mitteil. Deutsch. Entomol. Gesell., E.V.* 7: 90–96.

Mannheims, B. J. 1938. Uber das vorkommen der Gattung *Curupira* in Manschukuo (Diptera: Blepharoceridae). *Arbeit. über Morph. und taxonom. Entomol.* 5: 328–332, 3 figs.

Mannheims, B. J. 1954. Die Blepharoceriden Griechenlands und Mitteleuropas (Dipt.). *Bonn Zool. Beitrage* 1: 87–110, 8 figs., 2 pls.

Müller, Fritz. 1879. A very curious dipterous insect. *Trans. Ent. Soc. London, Proc.* 1879: 4.

Müller, Fritz. 1881. On female dimorphism of *Paltostoma torrentium. Entom. Monthly Mag.* 17: 225–226.

Müller, Fritz. 1881. A metamorphose de um insecto Diptero. *Arch. do Mus. nac. de Rio de Janeiro* 4: 47–85, 147–151, 4 pls. [*Paltostoma torrentium*]

Osten Sascken, C. R. 1874. Report on the Diptera collected by Lieut. W. L. Carpenter in Colorado during the summer of 1873. *In* Hayden's U.S. Geol. and geog. Survey of Colorado for 1873, pp. 561–566. [*Bibiocephala*]

Osten Sacken, C. R. 1880. Dr. F. Müller's discovery of a case of female dimorphism among Diptera. *Entom. Monthly Mag.* 17: 130–132.

Osten Sacken, C. R. 1891. Synopsis of the described genera and species of the Blepharoceridae. *Berlin. entomol. Zeitschr.* 36: 407–411.

Osten Sacken, C. R. 1895. Contributions to the study of the Liponeuridae Loew (Blepharoceridae Loew, olim). *Berlin. entomol. Zeitschr.* 40: 148–169. [*Curupira*]

Paulian, Renaud. 1953. Faune des eaux douces de Madagascar. II. Larves de Blepharoceridae (Dipt.). *Mem. Inst. Scient. Madagascar* (E) 4: 431–441, 15 figs. [Eight larval types]

Röder, V. von. 1890. Zwei neue nordamerikanische Dipteren. *Wien. Entomol. Zeitg.* 9: 230–232. [*Agathon*]

Schnuse, W. 1901. Bemerkungen uber *Apistomyia elegans* Big. *Zeitschr. Hym. Dipt.* 1: 145–149, 16 figs.

Scott, Hugh, and C. G. Lamb. 1915. The early stages of *Paltostoma schineri*, Williston (Diptera, Blepharoceridae). *Ann. Mag. Nat. Hist.* (8) 15: 181–202, 17 figs.

Steinmann, Paul. 1907. Die Tierwelt der Gebirgsbäche, eine faunistischbiologische Studie. *Ann. biol. Lacustre* 2: 72–163. [*Liponeura brevirostris*, pp. 99–103]

Stuckenberg, Brian R. 1955. New Blepharoceridae from South Africa. *Ann. Natal Mus.* 13: 175–209, 11 figs. [Re-definition of *Elporia*]

Tillyard, R. J. 1922. A revision of the New Zealand Blepharoceridae (Order Diptera). *N. Zeal. Journ. Sci. & Tech.* 5: 101–107, 3 figs. [*Paracurupira*]

Tillyard, R. J. 1922. Australian Blepharoceridae (Order Diptera). Part 1. Description of new species. *Austral. Zoologist* 2: 159–172, 7 figs., 2 pls. [for Parts 2 and 3, see Tonnoir]

Tonnoir, A. 1923. Australian Blepharoceridae. Part II. Larvae and pupae. *Austral. Zoologist* 3: 47–59, 7 figs. [for Part 1, see Tillyard]

Tonnoir, A. 1923. Australian Blepharoceridae. Corrections and additions to Parts I and II. *Austral. Zoologist* 3: 135–142, 5 figs.

Tonnoir, A. 1924. Les Blepharoceridae de la Tasmanie. *Ann. biol. Lacustre* 13, fasc. 1–2: 5–67, 28 figs.

Tonnoir, A. 1930. Notes on Indian blepharocerid larvae and pupae, with remarks on the morphology of blepharocerid larvae and pupae in general. *Rec. Indian Mus.* 32: 161–214, 58 figs. [*Euliponeura; Horaia*]

Tonnoir, A. 1931. Notes on some types of Indian Blepharoceridae. *Rec. Indian Mus.* 33: 283–289, 8 figs.

Tonnoir, A. 1932. Notes on Indian Blepharoceridae. III. *Rec. Indian Mus.* 34: 269–275, 2 figs.

Walley, G. S. 1927. Review of the Canadian species of the dipterous family Blephariceridae. *Canad. Ent.* 59: 112–116.

Williston, S. W. 1893. Diptera brasiliana III. A new genus of Blepharoceridae. *Kansas Univ. Quart.* 1: 119–120. [*Snowia*, now *Kelloggina*].

DISCUSSION

Ashley B. Gurney. Would you please comment on the so-called "bursting-out" emergence of adults from the pupae?

C. P. Alexander. The emergence from the pupa is not instantaneous, as has been assumed but is a more gradual process. The adult fly, in emerging, hangs to the pupal exuvium by its strong legs and does not release its hold until the wings are fully expanded, a question of minutes or less.

R. L. Usinger. How does the distribution of Blepharoceridae correspond to distributional patterns in the Deuterophlebiidae and Maruina?

C. P. Alexander. Both groups mentioned above show the same disjunct distribution as do certain genera of the Blepharoceridae. Such a type of distribution may be actual but in many cases are due to insufficient knowledge. The gaps gradually will be filled.

John D. Lattin. While the Deuterophlebiidae are generally considered to be montane in habitat, one species is known from a valley stream in the Willamette Valley in Oregon at an elevation of about 100 feet. The stream was a rather slow-moving one.

C. P. Alexander. Most of the known Deuterophlebiid larvae do occur in mountainous areas but in Japan have been taken at lower altitudes but, according to my remembrance, still in lotic conditions. I do not recall other species occurring in slow flowing streams, i.e. approaching lenetic conditions. The recently discovered species in Chile may occur in quiet streams.

The Geographical Distribution of the Coccoidea

By G. F. Ferris
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ABSTRACT

To be valid and useful any conclusions concerning the geographical distribution of any group must be based upon a sound taxonomy and adequate collecting. The degree to which the world has been searched for members of the Coccoidea is considered. The taxonomy was, until a period which began some years ago, thoroughly inadequate and misleading. At the present time a few genera have been clarified to a degree which permits what seem to be probably valid conclusions. Examples of such genera are cited and general conclusions which can be drawn from them are given.

The Geographic Distribution of the Scopariinae (Lepidoptera: Pyralidae)[1]

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ABSTRACT

The Scopariinae are a compact subfamily of several hundred species, related to the Nymphulinae and Odontiinae and probably also to the Crambinae. The group is primitive and probably of great age. It has endemic developments on most oceanic islands, but is well represented on the continents, too. Most of the known larvae feed on mosses, on grass-roots, and on roots of dicotyledonous plants. Scoparia *has a wide range in the Holarctic, extends into tropical Africa and through the Oriental and Neotropical regions and has endemic developments in Australia, New Zealand, Chile, and the Falkland Islands. The New Zealand endemics* Tetraprosopus *and* Xeroscopa *are segregates of* Scoparia. Scoparona *is a circumpolar boreo-alpine derivative of* Scoparia. Eudoria *is nearly world-wide, though it has no arctic species. Its success in colonizing oceanic islands is perhaps related to its moss-feeding habits. It has large endemic developments in New Zealand and Hawaii, smaller ones in other island groups, and good representation in most continents. Genus A is a New Zealand endemic. The Palaearctic* Witlesia *is a minor segregate of* Eudoria; Dipleurina *is more distinct.* Eclipsiodes *is an Australian genus with "flash" coloration on the hind wing. Genus B is another Australian endemic.* Dasyscopa *has a wide range in the Oriental region, but few species.* Micraglossa *ranges widely in the Oriental and Papuan regions, with several scattered endemic species, and with a large and hitherto unsuspected endemic development in New Guinea, including Genera C, D, and E.* Phenacodes *is a Papuan-Australian genus of giant species.* Anarpia *is a Mediterranean endemic; Genus F is Sonoran and Cordilleran; Genus G is confined to St. Helena.* Mestolobes, Promylaea, Elusia *and* Lissophanes *belong to other subfamilies. The general distribution pattern shows an unusual capacity for dispersal, combined with local specialization and radiation and overall conservatism.*

The Scopariinae are a very primitive subfamily, standing near the point of origin of the large pyraustine-nymphuline complex, and showing similarities to the lower Crambinae. Though the subfamily is very uniform in structure and habitus, it has a large number of species, many of them grouped in endemic regional complexes: there seems to be rapid speciation in favourable environments. Similarly, though the range of the group as a whole and of some of its genera is very wide, extending from the subarctic to the subantarctic zones, the ranges of individual species and groups are often closely restricted. One of the striking distributional features is the presence of the subfamily in a large number of oceanic islands, including the Faeroes, Bermuda, the Azores, the Canaries, Madeira, St. Helena, the Falklands, Juan Fernandez, Rapa, Tahiti, the Marquesas, Hawaii, the Kermadecs, Chatham, Auckland and Norfolk islands, Réunion and Mauritius.

Before the distribution is discussed in greater detail it will be necessary to outline the classification, as a natural generic arrangement has been published only for the European fauna (Chapman, 1911; Marion, 1954). The main divisions recognized by Chapman prove to be well founded; his two largest genera, *Scoparia* Curtis and *Eudoria* Chapman, are constantly separable and numerously represented over a very wide range; *Witlesia* Chapman is hardly distinct from *Eudoria*, but *Scoparona* Chapman, *Anarpia* Chapman and *Dipleurina* Chapman are all natural groups, though all three are restricted in size and range. *Cholius* Guenée has been shown by Marion to be a pure synonym of *Scoparia*. Of the non-European genera recognized by Hampson and subsequent authors, *Mestolobes* Butler, *Promylaea* Meyrick, *Elusia* Schaus, and *Lissophanes* Warren should be removed from the Scopariinae; Dr. Elwood C. Zimmermann writes me that he became aware of the separate position of *Mestolobes* some time before I did; the credit for the discovery should therefore go to him. *Mestolobes* will in my opinion go close to *Cybalomia; Promylaea* is evidently a close relative of *Mestolobes*. *Elusia* also appears to be related to *Cybalomia* though not directly to *Mestolobes*. *Lissophanes* has been shown by Martin (1955) to be a glaphyrine. The type species of *Xeroscopa* Meyrick and *Tetraprosopus* Butler have genitalia of the normal *Scoparia* configuration, but most of the species placed by Hampton (1897) in *Xeroscopa* have *Eudoria*-type genitalia. The amount of hairy vestiture on the hind wing is evidently an unreliable guide to relationship and *Xeroscopa* and *Tetraprosopus* are best sunk to *Scoparia* and their species distributed according to affinity. I have not examined sufficient material of *Eclipsiodes* to determine its status, except that it is clearly scopariine. *Dasyscopa* Meyrick is a natural genus with a few species. *Phenacodes* Turner is a very distinct genus, with a few Papuan species in addition to the type species from Queensland. *Micraglossa* proves to have a considerable number of species, mostly Papuan; these appear to belong to at least four distinct groups, probably closely related; these are *Micraglossa*, s.s., and genera C, D, and E. Four other very distinct genera are recognizable: Genus G includes all species examined from St. Helena; Genus A includes *epicomia* Meyrick, from New Zealand; Genus B includes *spelaea* Meyrick, from Australia; Genus F includes the group of *delphusa* Druce and *tricoloralis* Dyar, from Central America and western North America. I will describe these genera and discuss the taxonomy of the group in a separate paper, but the general relationships appear to be as follows: *Scoparia* and *Scoparona* form one major division; a second is formed by *Eudoria*, with its relatives or derivatives *Dipleurina*, *Anarpia* and *Dasyscopa;* the remaining smaller groups (excepting *Eclipsiodes*, which I have not examined in detail) all show a certain similarity, especially in the somewhat spatulate form of the uncus, but they also have profound differences, and it is uncertain whether they should be considered as relicts of a once widespread type, or as somewhat convergent local developments.

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The largest and most widely distributed genus is *Eudoria* (Fig. 1). This occurs throughout the subarctic and boreal zones of the Holarctic region, where it is represented by one or two very wide-ranging species. In the north temperate zone the distribution is more patchy: there are about half-a-dozen species of general or western European range, one or two of them perhaps extending to Siberia and Amur; there are several alpine or boreo-alpine species, at least one Lusitanian one (*angustea* Stephens) and probably a few Mediterranean ones; in the eastern Palaearctic there are a number of poorly known species; in western North America several more; and in eastern North America two or three. The range of *Eudoria* in the tropics is not well known. It is evidently widely distributed in the cool moss-forest zone; I have seen species from Bolivia, Sao Paulo, Cameroons, the Himalayas and Java; a species is known from the Malgassic region. Further study and collecting will undoubtedly greatly extend this record, but the genus is evidently absent or poorly represented in Chile and Patagonia. The greatest development of the genus is in the Pacific region; seven of the eight Australian species of *Scoparia* s.l. I have examined belong to this genus as do 20 out of 29 New Zealand species and all species examined from Tahiti, Austral Islands, Marquesas and Hawaii. If these proportions are extrapolated to the total of described species, the following figures for the probable number of described species of *Eudoria* are obtained:

Australia	45
New Zealand and outlying islands	80
Rapa	2
Tahiti	2
Marquesas	7
Hawaii	64

One species is said to be shared by Australia and New Zealand, but otherwise the species are all endemic in their own island-groups. *Eudoria* also occurs on Atlantic islands: the Azores, Canaries and Madeira, but not, so far as known, on St. Helena or the Falklands. I have not examined Scopariinae from Juan Fernandez. All Chilean Scopariinae I have studied belong to *Scoparia*, s.s.

Some striking features of the distribution just described are the apparent absence of the genus from temperate South America, its rather sparse representation in the continental tropics, and the large species-swarms in New Zealand and the Hawaiian Islands. The apparent absence of *Eudoria* in the Papuan region is probably not significant, as there is a rich and almost unknown fauna of Scopariinae in the mountains of New Guinea: the absence from the large western Pacific islands of Fiji and Samoa is, however, significant and striking, for their fauna of Pyralidae is rich and fairly well known.

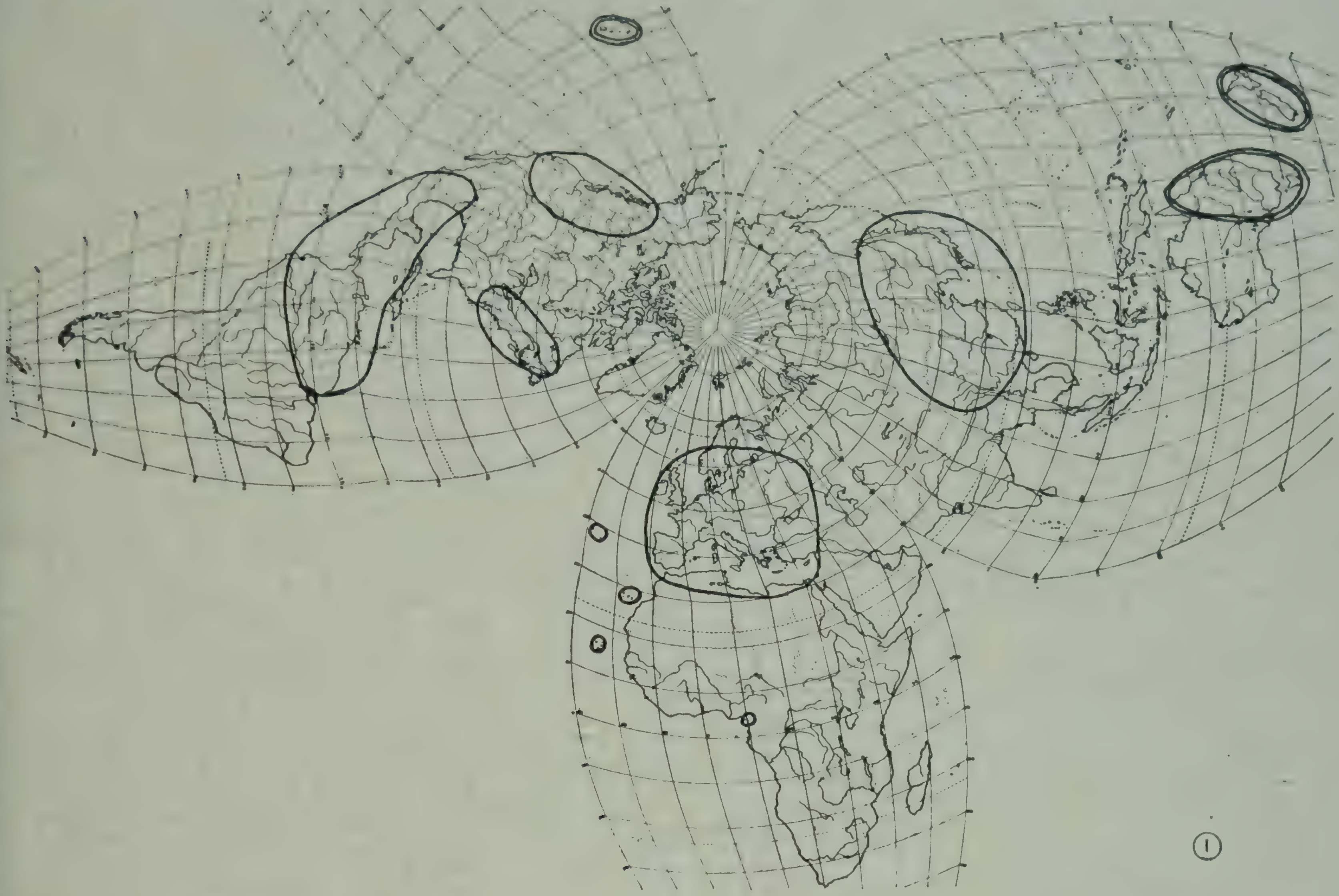

Fig. 1. Distribution of the genus *Eudoria*. The total range, not outlined, is largely continuous except for water-gaps, but apparently does not extend to temperate South America or to the western Pacific islands. The circled areas are centres of endemism; those circled twice have particularly large numbers of species.

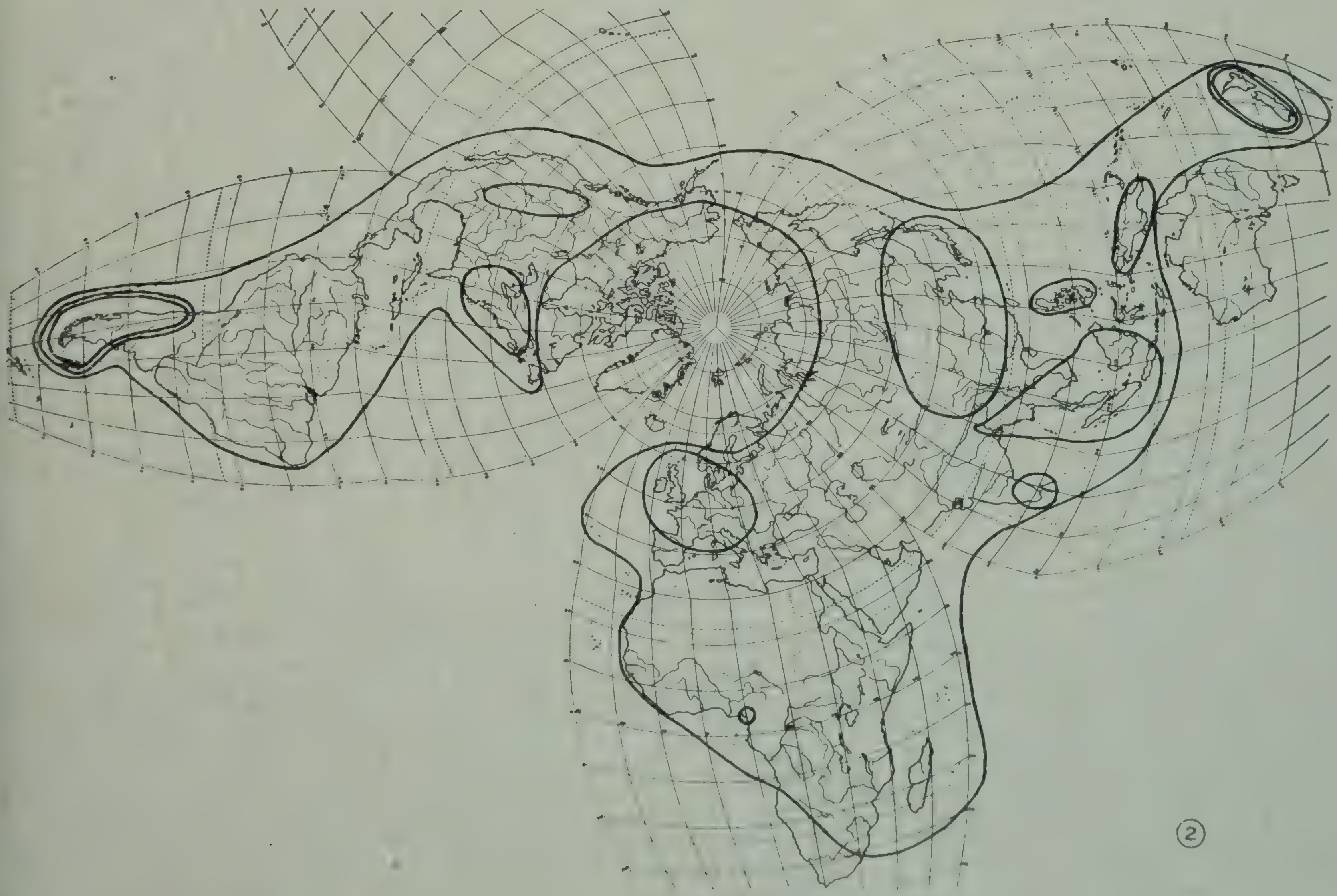

Fig. 2. Distribution of the genus *Scoparia*. Conventions as in Fig. 1, but the total range is outlined as well as centres of endemism.

The genera related to *Eudoria* are all small and restricted in range: *Dipleurina* has only one known species, occurring definitely in western Europe and said to range to Ussuri and western China, though these eastern extensions must be regarded with suspicion; *Anarpia* (Fig. 4) has two or three species from the Mediterranean-Iranian region; *Dasyscopa* (Fig. 4) has a small number of species in the Malayan region and is said to have one in the Loyalty Islands.

The genus *Scoparia* has nearly as wide a range as *Eudoria*, but has not been so successful in colonizing oceanic islands, and is poorly represented in Australia and tropical America. There are several species in western Europe, some of which are said to extend to the eastern Palaearctic region, but again the latter records require confirmation; there are certainly several endemic species in China and Japan. In North America there is one widespread species, a small endemic complex in the east and another in the dry areas of the west. There are species in tropical America, a considerable endemic development in Chile and Argentina, and at least one species in the Falkland Islands. This genus occurs on Mt. Cameroon and probably elsewhere in continental Africa, and also in the Malgassic region. It is well represented in the mountainous parts of the Oriental and Papuan regions, and, though unknown in Australia, has a considerable endemic development in New Zealand. It is unknown from Polynesia. It is absent from the subarctic zone, but is represented there by the monotypic Holarctic genus *Scoparona* (Fig. 3) which extends far south along mountains in both Old and New worlds.

The *Micraglossa* group (Fig. 3) has a few species in the Indo-Malayan area; so far as known there is little local endemism in this area, and all species examined belong to *Micraglossa*. In the mountains of New Guinea there is a strong local development of this group, at least fifteen species being present in the small sample brought back by the Kaiserin-Augusta-Fluss expedition. *Micraglossa* s.s. and genera C, D and E are all represented in New Guinea.

Phenacodes (Fig. 4) has one species in Queensland, two or three in New Guinea; these are abnormally large and robust, and resemble Epipaschiinae; the larvae are atypical, in that they feed externally on ferns at night, hiding in burrows in the peat by day. Genus B (Fig. 4) is Australian, living, according to Meyrick, in mossy places under rock-overhangs. Genus A (Fig. 4) is represented by a single known species, said to occur in both New Zealand and the Kermadec islands; if the latter record is trustworthy, perhaps it represents an artificial introduction. Genus G seems to represent an old immigration to St. Helena. Genus F (Fig. 4) is the most divergent in genitalic structure of all the genera; its endemic range in the Sonoran-Californian-Vancouveran area is unusual.

Eclipsiodes (Fig. 3) is said to have a considerable development in Australia. As I have examined only the type species, I cannot say whether the genus as now conceived is a natural one.

The distribution of the Scopariinae is remarkable from several standpoints. As already mentioned, the range of the group as a whole is very wide. The rather confined ranges of most of the species suggest that this extensive collective range is the result of occasional long-range colonization rather than of regular wide dispersal. This is confirmed by the development of species-swarms not only in oceanic or semi-oceanic islands such as Hawaii or New Zealand, but also in less remote islands such as New Guinea and the Philippines, and probably in mountainous or forested parts of most of the continents as well. The weak flight and often secretive habits of the adult moths do not seem well-adapted to wide dispersal. On the other hand, the known larvae of *Eudoria* tunnel in mosses on tree-trunks, and could easily be transported by rafting. It is noteworthy that this genus occurs on more remote oceanic islands than the genus *Scoparia*, whose known larvae feed on roots. However, even *Scoparia* reaches the Azores and Falkland Islands, and it must be pointed out that the life histories are known only for a few European species, and that some of the other species may well turn out to feed on mosses or lichens. One would suspect from their habitats that several of the other genera also have moss-feeding larvae.

Species-swarms in this subfamily appear to develop most readily in fairly large habitats under semi-isolated conditions which presumably imply relaxed competition—on a large scale in Hawaii, on a much smaller scale on the Marquesas and Rapa, on a very large scale in New Zealand, on a more modest scale in Australia and Chile, and in the mountains of New Guinea and of Equatorial Africa. One of the puzzling features is the apparent absence

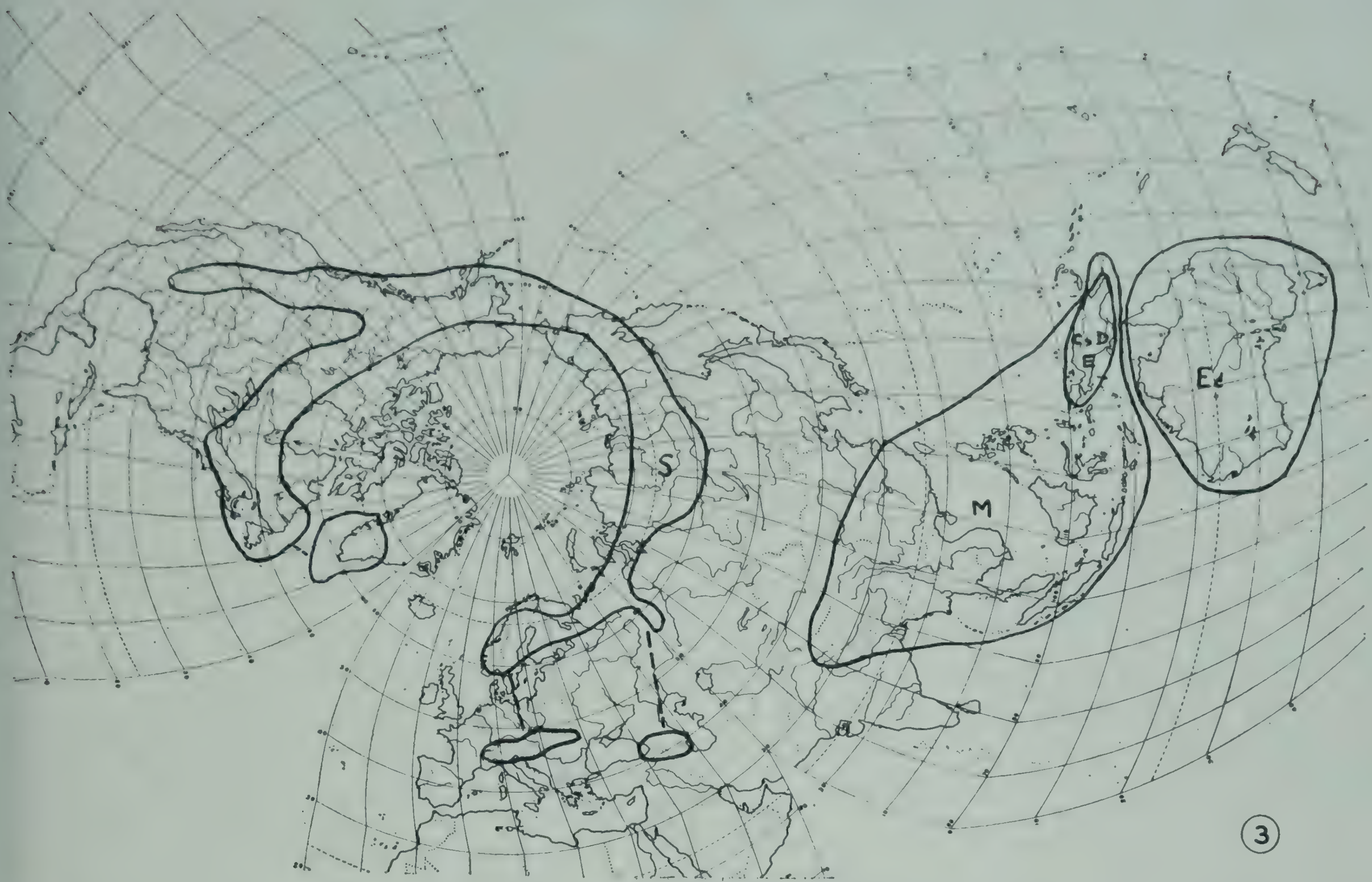

Fig. 3. Ranges of scopariine genera. S = *Scoparona;* Ec = *Eclipsiodes;* M = *Micraglossa;* C, D, E = genera, C. D. and E (segregates of *Micraglossa*). The total ranges are circled.

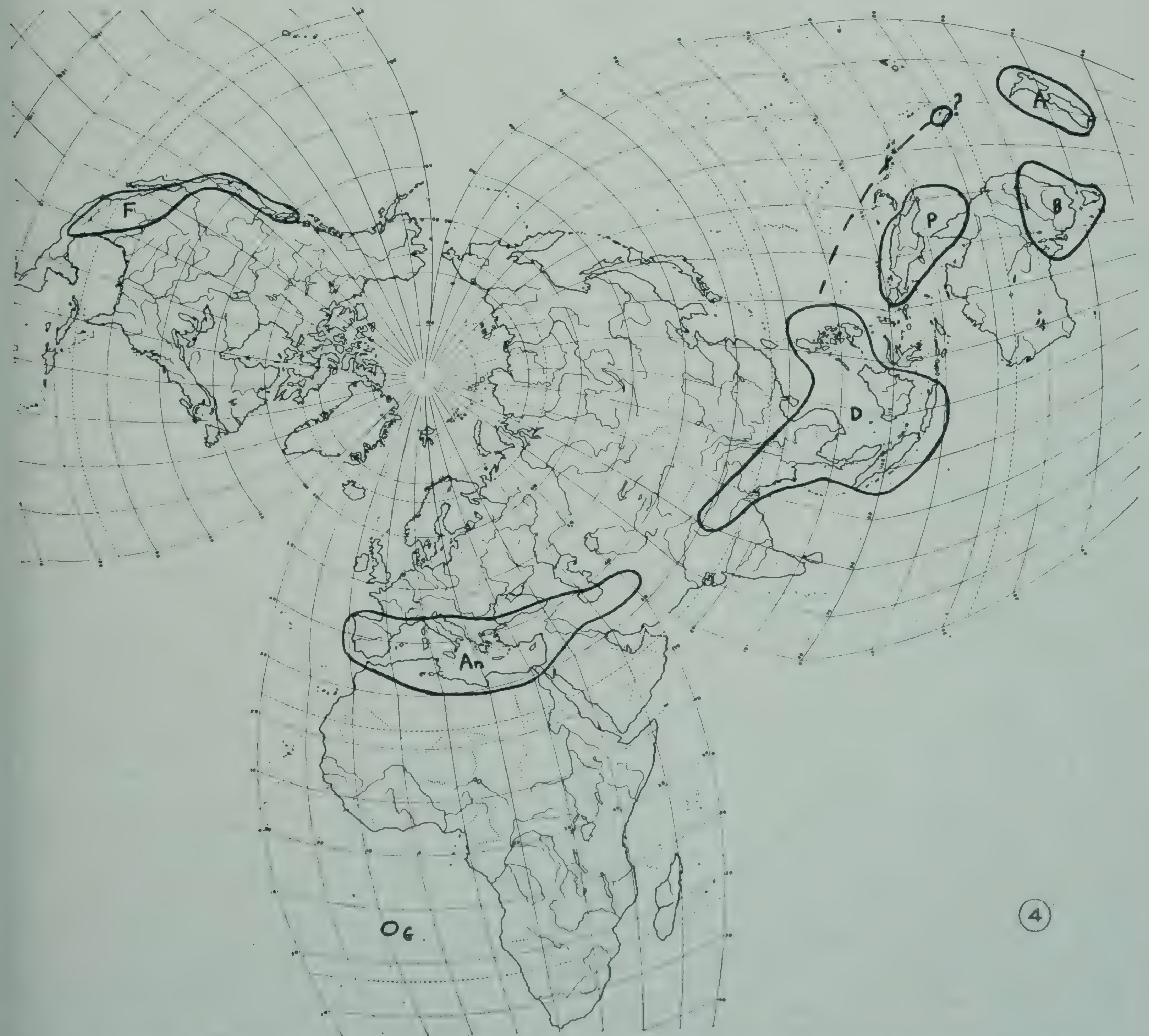

Fig. 4. Ranges of scopariine genera. A = Genus A; An = *Anarpia;* B = Genus B; D = *Dasyscopa;* F = Genus F; G = Genus G; P = *Phenacodes.*

of the group in Fiji and Samoa, both large islands with rich developments of other pyralid subfamilies.

Because of the very uniform basic structure and habitus, it is so far impossible to reach satisfactory conclusions as to the phylogeny either of the group as a whole or of its constituent genera. On the whole it seems likely that *Eudoria*, in spite of the simplicity of its genetalic structure, is an advanced genus. The beak-like uncus of *Scoparia* is probably more primitive than the hood-like one of *Eudoria*—though the latter is paralleled in the subfamily *Odontiinae*—and the spine-like termination of the sacculus of *Scoparia* is found in several divergent genera, as well as in the probably nymphuline genus *Neurophyseta*. However both major groups are so widely distributed that this phylogenetic conclusion has no geographic significance.

There is little doubt that most major areas have their own species-groups. The relationships of these from area to area are usually hard to determine. The species of *Eudoria* in the Marquesas and Rapa appear to be related to those of Hawaii, and this complex as a whole resembles certain New Zealand species, but the more primitive Hawaiian species are very generalized, and an American origin cannot safely be ruled out. Both New Zealand and Australia have striking endemic developments, with an unusual degree of pattern-modification—undoubtedly the result of special cryptic adaptations. The large endemic developments of New Guinea appear to be local radiations of rather widely distributed Indo-Malayan groups—both the *Scoparia* species and the *Micraglossa* complex being represented, though probably by fewer species, in the Philippines and on the continent of Asia. The Chilean species of *Scoparia* tend to show special crypsis, like those of New Zealand; there is no obvious direct relationship between the species of the two faunas, but the absence or poor representation of the genus in Australia and tropical South America might be taken as an indication of an Antarctic dispersal history.

It is obvious that this and many other detailed aspects of the distribution of the Scopariinae can be discussed intelligently only after study of a more representative range of species. Indeed, it is likely that more intensive collecting of these often obscure and secretive insects will revolutionize the distributional picture for some tropical areas, as very incomplete studies are already doing for the Malayan and Papuan subregions. Nonetheless, the general outline presented here will certainly accommodate the majority of species and genera, and provides most gratifying support and amplification for Chapman's pioneer study.

REFERENCES

Chapman, T. A., 1911. On the British (and a few Continental) species of *Scoparia* Hw. *Trans. Ent. Soc. London*, 1911: 501-518, Pl. 35–44.

Hampson, Sir G. F. 1897. On the classification of two subfamilies of moths of the family Pyraladae: the Hydrocampinae and the Scoparianae. *Trans. Ent. Soc. London*, 1897: 127–240.

Marion, H. 1954. Révision des Pyraustidae de la faune française. *Rev. Franc. Lép.* 14: 181–188.

Martin, E. L. 1955. [note on *Lissophanes*] *Pyralis*, No. 2 [privately circulated].

DISCUSSION

GEO. STEYSKAL. What are the relationships of the species of the disjunct South American area?

E. MUNROE. As now seen these appear to form an endemic species group. There is nothing against a pre-pleistocene path to New Zealand via Antarctica. The ability of this group to thrive in cool, wet climates and its ocean-crossing abilities would favour such a path, but it is not impossible that they came via mainland South America whose fauna is still poorly known, and where extinction might easily take place.

GEO. STEYSKAL. Do the insects occur in Java and Sumatra and in the Philippine Is., where the map shows only a narrow connection with New Guinea and Australia?

E. MUNROE. The limits shown are merely peripheral and do not attempt to indicate relationship. The fauna of Java and Sumatra is commensurately wide, and as far as known is of Malayan type. The Philippine Scopariinae have relations to both Indo-Malaya and New Guinea, but so far as known no direct relations to Australia.

J. L. GRESSITT. (a) Is group represented in New Caledonia? (b) Is New Guinea fauna related to that of New Zealand?

E. Munroe. (a) I have no record of the group from New Caledonia. (b) So far as I have examined them, these two faunas seem quite distinct.

Harry K. Clench. Is there any special development of the Scopariinae in cloud forest region? If so, please comment on those of Mt. Apo and adjacent mountain regions of Mindanao.

E. Munroe. The tropical groups seem highly developed in the cloud-forest environment. The fauna of Mt. Apo is closely similar to that of New Guinea, but is not yet known to share any species of Scopariinae, and shows much fewer species in a fauna of similar size.

W. H. Lange. (a) Are the moss-feeding types primitive or advanced and (b) are any aquatic?

E. Munroe. (a) We don't yet know enough about either phylogeny or life-history to generalize about this. (b) No aquatic forms are known to me.

Remarques sur la Faune entomologique des Antilles françaises

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Les Antilles françaises comprennent deux grandes îles: la Martinique et la Guadeloupe, plus quelques groupes de petites îles qui sont très proches de la Guadeloupe, la Désirade, Marie-Galante, les Saintes, et à 200 kilomètres au nord Saint-Barthélémy et Saint-Martin, cette dernière partagée entre la France et la Hollande.

Christophe Colomb à son 2e voyage découvrit d'abord une petite île qu'il nomma La Desirada, puis une autre, dédiée à Marie (Maria Gratiosa, nom devenu par altération Marie-Galante), ensuite le ler novembre deux îles qu'il appela Los Santos (devenues les Saintes), enfin une grande terre qu'habitaient les Caraïbes, et qu'il appela Nuestra Senora de Guadalupa, en hommage à un célèbre pélerinage espagnol, nom conservé sous la forme de: la Guadeloupe.

Ces îles sont situées au centre des Petites-Antilles, vaste arc-de-cercle qui réunit les Grandes-Antilles (Cuba, Puerto-Rico, Jamaïque, etc.) au continent sud-américain par le Venezuela.

Elles sont avant tout de nature éruptive, avec des volcans encore actifs: à la Guadeloupe la Soufrière qui n'émet que des fumerolles, et à la Martinique la Montagne Pelée, parfois en éruption, celle de 1902 détruisant totalement la ville de Saint-Pierre, Le caractère volcanique explique en grande partie les caractères et la nature de la faune de ces îles. Cependant il y a par endroits des dépôts sédimentaires, notamment à Saint-Barthélémy, et à l'une des parties de la Guadeloupe.

La Guadeloupe qui a une aspect très particulier, comprend deux terres très différentes, l'une, la Guadeloupe proprement dite, est un massif montagneux très accidenté, couvert en entier par une immense forêt où la densité de la végétation rend l'intérieur impénétrable, et presque inexploré; la population, assez dense, est confinée sur la bande côtière dont la végétation est constituée par des arbres tropicaux, pour la plupart introduits: cocotier, manguier, arbre-à-pain, goyavier, etc, dans les parties les plus irriguées on cultive intensivement le bananier. L'autre terre, appelée "Grande Terre" est au contraire très plate, c'est le domaine de la canne à sucre.

Plus au sud et séparée de la Guadeloupe par la Dominique, possession anglaise, la Martinique quoique montagneuse a l'intérieur plus accessible; sillonnée de routes très pittoresques (l'une traverse une forêt de Fougères arborescentes).

Si la flore de ces îles est bien connue, et par ailleurs assez riche (au moins 3000 espèces de plantes phanérogames), la faune a peu retenu l'attention des naturalistes, et a été l'objet de peu de travaux. Il faut dire que dans l'ensemble cette faune est très pauvre, le monde animal semblant comme écrasé par l'exubérance du monde végétal. C'est ainsi qu'il n'y a pas un Mammifère indigène, et qu'on n'a pu y dénombrer que 122 espèces d'Oiseaux, ce qui est fort peu pour des terres situées sous les tropiques.

L'inventaire de la faune entomologique des Antilles françaises n'a pas encore été fait d'une manière satisfaisante, sauf peut-être pour les Coléoptères, comme on le verra plus loin.

Les Myriapodes paraissent nombreux et variés; la grande Scolopendre, qui a des espèces dans le monde entier, est commune; sa morsure est fort désagréable.

Il y a des Crustacés terrestres, et on est surpris de voir courir sur le sol des forêts humides, très loin de la mer, un Bernard l'Ermite qui se loge dans des coquilles d'Escargot. Dans les mares plus ou moins saumâtres grouille par milliers un très petit Crabe du genre *Ucca*; de même que beaucoup d'autres une de ses pinces est atrophiée, l'autre au contraire très développée; comme il l'agite sans cesse devant sa tête, les créoles lui ont donné le nom pittoresque de "c'est-ma-faute".

Parmi les Arachnides, les Scorpions sont très rares; on trouve parfois l'*Isometrus maculatus*, espèce cosmopolite; il y en a probablement un autre.

Les Phrynes sont abondamment représentées par *Tarentula palmata*, commune même dans les petites îles. Son aspect redoutable la fait craindre, bien à tort puisqu'elle n'a pas de venin et est au surplus inoffensive. J'ai tout lieu de croire qu'elle est souvent signalée comme "l'Araignée des 24 heures" dont la morsure serait fatale dans un temps très court, mais on ne peut en relever un cas précis, bien entendu, et c'est une légende injustifiée. On pourrait penser à une confusion avec la "Veuve noire (Black widow)" Araignée américaine venimeuse, mais sa présence n'est pas certaine, et on ne la connaît pas avec certitude des Petites Antilles. On a décrit des Tartarides (Arachnides) de la Martinique, et je les ai retrouvées à la Guadeloupe.

Les Araignées sont assez abondantes, du moins en individus, plus qu'en espèces; elles sont jusqu'à présent très mal connues et on a signalé à peine 10 espèces, ce qui est manifestement insuffisant. J'ai eu la satisfaction de voir près de Fort-de-France une très belle Mygale: *Avicularia versicolor* grosse comme la paume de la main; elle vit dans des coques de soie épaisse, parcheminée, tissée dans le creux de certains arbres; en tapotant la coque avec la main, on les fait sortir; la Mygale court sur le tronc lisse et prend l'attitude de défense: l'avant corps et les deux paires de pattes antérieures relevées, les chélicères ouvertes; malgré cela elle n'est pas dangereuse, et elle est peu agressive. Le terme de "belle" n'est pas excessif pour cette Araignée, car malgré la couleur sombre des Mygales elle a des reflets très brillants, dus au pelage vert-de-gris qui recouvre son céphalothorax, et aux poils irisés dont ses pattes sont abondamment pourvues.

Une Araignée commune est *Argiope argentata*, qui se trouve dans une grande partie du continent américain et dans toutes les îles; l'attitude des Argiopes est invariable, quel que soit le pays: elles se tiennent au centre d'une grande toile géométrique verticele, à une faible distance du sol, la tête en bas, les 8 pattes ambulatoires réunies 2 par 2 formant ainsi un grand X; la toile a presque toujours un stabilimentum, ruban épais de soie en zigzag qui probablement consolide la toile.

On trouve aussi en abondance, aussi bien à la Martinique qu'à la Guadeloupe, *Gasteracantha tetracantha*, qu'on appelle là-bas "l'Araignée triangulaire"; sa toile géométrique, tendue sur les arbustes à un mètre ou deux du sol, s'inscrit dans un cadre rectangulaire fait de fils assez forts avec un petit épaississement de soie très régulièrement tous les 3 ou 4 centimètres; c'est un fait constant que les Gastéracanthes ont des toiles ornées. Ce genre, caractéristique de la faune tropicale du monde entier, compte peu d'espèces en Amérique où il est remplacé par le genre voisin *Micrathena*, exclusivement américain, qui s'est développé en un grand nombre d'espèces très variées en formes et en couleurs. Les *Micrathena* représentent un genre se substitution, peut-on dire, qui a pris la place des *Gasteracantha*, celles-ci étant surtout de l'Ancien monde; le remplacement de genres par d'autres est un fait assez fréquent: l'Amérique présente souvent des genres qui lui sont spéciaux, mais sont très voisins de genres de l'Ancien monde: parmi les Hyménoptères on peut citer les *Monedula*, américains, qui sont tout à fait semblables par la forme et par le comportement aux *Bembex* de l'Ancien monde, ou encore le genre *Pepsis* qui est comparable aux *Hemipepsis*, *Cryptochilus*, *Cyphononyx* d'Afrique et d'Asie.

En ce que concerne les *Micrathena*, on est surpris de ne pas les trouver aux Antilles françaises, ni semble-t-il dans toutes les Petites Antilles, car ils peuplent tout le continent sud-américain et central jusqu'au Mexique. De même les *Nephila*, grosses Araignées si caractéristiques des tropiques, ne s'y trouvent pas. Les absences de formes sont plus remarquables dans les îles que la présence.

Un certain nombre d'Araignées, parmi lesquelle on peut signaler les Pholcidae, Theridiidae, Argiopidae, semblent abondantes; par contre les Salticidae sont peu nombreuses, ce qui est surprenant car elles sont un élément dominant parmi les Araignées, surtout dans les régions tropicales. Il y a aussi de grosses Sparassidae (parmi lesquelles l'universelle *Heteropoda venatoria*), qui le plus souvent vivent dans une coque de soie parcheminée sur les feuilles des arbres, et non sous les pierres comme le font celles de la région saharienne.

D'une façon générale, pour les Araignées, c'est la faune cachée qui domine et on est surpris de voir si peu de formes vivant en plein air: les arbustes et plantes basses montrent très peu de toiles, certainement beaucoup moins qu'en Europe tempérée.

On peut actuellement donner la liste suivante des Araignées connues des Antilles françaises; elle représente environ le triple de ce qui était mentionné précédemment, mais il est évident que ce chiffre est encore très faible, par rapport à la réalité.

Avicularia versicolor Walck.
Eutychides guadelupensis Simon
Scytodes fusca Walck.
– *longipes* Lucas
Ariadna solitaria Simon
– *arthuri* Petrkw.
Artema atlanta Walck.
Physocyclus globosus Tacz.
Theridion rufipes Lucas
Leucauge argyra Walck.
– *venusta* Walck.
– *regnyi* Simon
Tetragnatha elongata Walck.
Cyclosa caroli Hentz
– *oculata* Walck.
Araneus nauticus L. Koch
Argiope argentata F.
Gasteracantha tetracantha L.
Selenops aïssa Walck.
Aysha tenuis L. Koch
Corinna scutulata Simon
Oxyopes salticus Hentz
Commoris enoplognatha Simon
Uloborus geniculatus Olivier
Oecobius benneri Petrkw.

En ce qui concerne les Insectes, il faut mettre à part les Coléoptères qui sont bien connus, grâce aux recherches de plusieurs entomologistes (notamment MM. Dufau, Lherminier, Vitrac) qui ont longtemps résidé à la Guadeloupe et fait des récoltes suivies et importantes. Mais sauf ce groupe, les Insectes sont mal connus.

Parmi les Coléoptères, la Guadeloupe se glorifie d'avoir un superbe Scarabéide, le *Dinastes hercules*, un des plus beaux exemples de dimorphisme sexuel qui soient: la femelle est quelconque, mais le mâle, plus gros qu'elle et mesurant jusqu'à 16 centimètres de long, a la tête prolongée par deux longues cornes placées dans un plan vertical; ce bel Insecte, qui n'est jamais commun, vit dans les forêts, d'où il sort quelquefois.

Chez les Orthoptères on trouve un grand Phasme, des Acridiens et d'assez nombreuses Sauterelles (Phasgonuridae) dont beaucoup vivent sur les arbres. Les Termites ont plusieurs espèces, aucune ne fait de constructions aériennes, mais leurs "chemins" se voient partout; ils ne semblent pas dévastateurs; leur taille est faible et leurs colonnes sont composées en majorité de *nasuti*.

Les Lépidoptères diurnes sont peu nombreux et c'est à peine si on en voit voler quelques-uns dans les bois. Mais les nocturnes (Phalènes, ou Moths) viennent abondamment aux lumières et j'ai pu en prendre un certain nombre, dont plusieurs ont déjà été l'objet d'études.

J'ai recherché particulièrement les Hyménoptères, sans grand succès. Seuls les Apidae sont assez communs avec les Xylocopes, Megachiles, Centris, ce dernier genre exclusivement américain. Il est assez intéressant de signaler que les Xylocopes ont souvent les deux sexes de couleur très différente, le mâle jaune, la femelle noire par exemple; or les antillais leur ont donné deux noms vernaculaires différents, n'ayant pas reconnu qu'ils sont de la même espèce. Les prédateurs, ou Guêpes *sensu lato*, sont peu nombreux, à part deux *Sphex* et deux *Sceliphron*, ces derniers tapissant de leur nid de terre gâchée les vérandas des maisons; les *Polistes* sont nombreux en individus, et nidifient au plafond des maisons. Comme partout les Fourmis sont innombrables. Malgré l'abondance de Lépidoptères nocturnes et de Coléoptères, dont les larves devraient servir de proies aux Hyménoptères parasites, j'ai trouvé très peu de ces derniers: en tout un Ichneumonide du groupe des Ophions, et un Chalcide.

Un Megachile, le *Megachile lanata* mérite une mention particulière. Très commun, il entre dans les maisons et établit son nid dans les trous des poutres. Cette espèce est surtout connue de l'Inde, mais on l'a trouvée aussi à l'île Maurice d'une part, et d'autre part aux Antilles. Elle a donc une répartition géographique assez étrange, mais qui peut, je crois, s'expliquer de la façon suivante: l'espèce est très probablement originaire de l'Inde, car c'est là qu'elle est le plus répandue. Mais les deux groupes d'îles où elle se trouve aussi ont reçu un peuplement humain important venant de l'Inde. On sait qu'à Maurice les originaires de l'Inde constituent une forte proportion de la population. Aux Antilles françaises, la proportion est moins forte, mais cependant il y a eu des immigrations hindoues: à la Guadeloupe, le village Matouba, près de Saint-Claude, en est composé presque uniquement. Or il est probable que les Indiens ont apporté avec eux des objets ménagers en bois, ou même des objets de culte car on voit par endroits de curieux très petits édifices religieux hindous faits en partie de bois. On peut supposer que des nids de *Megachile lanata* auraient été introduits dans ces conditions par l'Homme, ces Insectes nidifiant très souvent dans le bois.

Malgré la similitude de leur faune, les deux îles présentent parfois des différences assez remarquables. C'est ainsi que le *Polistes*, qui suspend de nombreux nids en papier aux plafonds des maisons, n'est pas le même: à la Martinique c'est *Polistes cinctus* qui fait un nid très allongé, jusqu'à 30 cm. x 6 cm., avec plusieurs centaines d'alvéoles; à la Guadeloupe c'est *Polistes versicolor* var. *multicolor*, à nid bien plus réduit, avec seulement 40 à 50 alvéoles, assez semblable en forme et en dimensions à celui des *Polistes* européens. Les *Pepsis* sont des Pompiles américains chasseurs de Mygales; à la Martinique on trouve le *Pepis dimidiata*, qui chasse probablement *Avicularia versicolor*; à Saint-Barthélémy c'est le beau *Pepsis rubra* à ailes écarlates (sa proie n'est pas connue).

Dans l'ensemble, la faune des Antilles françaises est fort pauvre, surtout relativement à celle des Grandes Antilles ou de l'Amérique Centrale qui est à la même latitude. Elle paraît avoir des affinités avec l'Amérique du Nord, plutôt qu'avec le continent sud-américain, et elle en caractérise bien plus par des absences que par la présence.

Die Tiergeographischen Verhältnisse Boliviens

Von W. Forster
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ZUSAMMENFASSUNG

Bolivien ist tiergeographisch gesehen wohl das interessanteste Land Südamerikas. Es ist grundsätzlich in zwei Teile gegliedert: Der tropische Teil und das Hochland der Kordillere. Im tropischen Teil findet sich die eigentlich "neotropische" Fauna, eine tropische Waldfauna, die sich offensichtlich, abgesehen von der Fauna des Westabhanges der Kordillere, der "Yungas", seit dem jüngeren Tertiär wenig verändert hat, reich an altertümlichen Arten mit zahlreichen nur in Südamerika vorkommenden Familien und Gattungen und verwandtschaftlichen Beziehungen zur afrikanischen, weniger zur indoaustralischen tropischen Waldfauna. Im Tieflande Boliviens grenzen drei Faunengebiete aneinander: Das Gebiet der amazonischen Fauna, die zentralbrasilianische Region und die Region des Gran Chaco. Dazu kommt die erwähnte Fauna der "Yungas", eine tropische Gebirgsfauna jungen Alters, die erst bei der im jüngeren Tertiär erfolgten Hebung der Kordillere enstanden sein dürfte. Die Fauna des Hochlandes, der waldfreien Gebiete über 3000m, zeigt nahe Verwandtschaft zu der holarktischen Fauna und scheint aus Formen zu bestehen, die erst nach der Hebung der Kordillere und dem Verschwinden der früheren tropischen Fauna aus der gemässigten Zone des Nordens eingewandert sind. Die heutige Verbreitung, sowie die Art- und Rassengliederung dieser Hochlandfauna dürfte weitgehend durch die eiszeitlichen Verhältnisse bewirkt sein.

Bolivien bildet, wie wohl kaum ein zweites Land Südamerikas, ein ideales Forschungsgebiet für den Biologen, da es innerhalb seiner Grenzen die gegensätzlichsten Lebensräume vereint. Hohe, eisgepanzerte Gebirge, die weiten Hochwüsten und Steppen des Altiplano, der abflusslosen Hochfläche zwischen Ost- und Westkordillere und die weiten Urwald- und Savannengebiete des tropischen Tieflandes, grössere Gegensätze innerhalb eines für südamerikanische Verhältnisse nicht sehr ausgedehnten Landes lassen sich kaum vorstellen. Zudem sind oft die gegensätzlichsten Lebensräume recht eng benachbart, wie z.B. die eisigen Gipfel und kalten Hochtäler der Kordillere und die heissen tropischen Regenwälder ihrer östlichen Täler.

Aus dem eben Gesagten geht schon hervor, dass Bolivien gerade für den tiergeographisch interessierten Zoologen von hohem Interesse ist und ich will Ihnen im Folgenden die vorläufig erarbeiteten Ergebnisse meiner Studien an Lepidopteren vortragen, die schon gewisse allgemeingültige Züge erkennen lassen.

Bolivien hat Anteil an den meisten der grossen tiergeographischen Gebieten Südamerikas. Zunächst sind grundsätzlich zwei Landesteile zu unterscheiden: Der tropische Teil des Landes und das Hochland der Kordillere oberhalb einer Höhenlinie von ungefähr 3000-3500m.

Im tropischen Teil finden wir diejenige Tierwelt, die im eigentlichen Sinne als "neotropisch", als "südamerikanisch" bezeichnet wird. Es ist im grossen gesehen eine tropische Waldfauna, die sich offensichtlich, abgesehen von der später zu besprechenden Fauna der Yungas, die die Gebiete am Osthang der Kordillere besiedelt, seit dem Tertiär nicht mehr wesentlich verändert hat. Sie ist reich an altertümlichen Arten mit zahlreichen nur in Südamerika vorkommenden Familien und Gattungen. Ich erinnere nur an die blauen Morpho, die Brassoliden, die Heliconier, die Ithomiiden und viele andere. Verwandtschaftliche Beziehungen, soweit solche überhaupt mit einiger Sicherheit festgestellt werden können, weisen nach der afrikanischen, auch nach der indoaustralischen tropischen Fauna, die ja gleichfalls noch ein weitgehend altertümliches Gepräge zeigen und ebenfalls zahlreiche, seit dem Tertiär kaum noch veränderte Formen enthalten. Nur am Rande sei hier bemerkt, ohne auf diese schwierige und sehr unstrittene Frage näher eingehen zu wollen und zu können, dass m.E. gerade die sogennanten mimetischen Formen nicht, wie nach den bekannten Theorien zu erwarten wäre, die am weitesten entwickelten, modernsten Glieder ihrer jeweiligen Gruppe sind, sondern im Gegenteil offensichtlich die ältesten. Doch würde es hier zu weit führen, auf diese Frage und die dadurch aufgeworfenen Probleme näher einzugehen.

Trotzdem die Tierwelt der tropischen Tiefländer Südamerikas im grossen gesehen eine weitgehende Einheitlichkeit aufweist, können doch verschiedene Faunengebiete festgestellt werden, für welche jeweils bestimmte Gattungen und Arten charakteristisch sind, oder häufiger, in denen die einzelnen Arten in verschieden ausgebildeten Unterarten vorkommen. Inwieweit, was sicher meist der Fall ist, diese tiergeographischen Gebiete ihrer Enstehung nach historisch zu erklären sind oder ob die heutigen unterschiedlichen klimatischen Verhältnisse die festzustellenden Differenzierungen hervorrufen, das zu entscheiden reichen unsere derzeitigen Kenntnisse noch nicht aus. Nur genaueste, über lange Zeiträume sich erstreckende Beobachtungen und unfangreiche, an Ort und Stelle durchzuführende Zuchtversuche und Experimente können erst die Grundlagen zu einer Klärung dieser Probleme liefern, zu deren Lösung auch die historisch-geologischen und die klimatischen Grundlagen teilweise erst noch zu erforschen wären.

Drei tiergeographische Gebiete grenzen im Tiefland Boliviens aneinander:

Von Norden her das Gebiet der amazonischen Hyläa, das auf bolivianischem Boden im Gebiet des unteren Rio Beni, des Acre-Gebietes und am unteren Rio Mamoré am reinsten ausgeprägt ist, aber auch das gesamte Tiefland Nordost- und Mittelboliviens, südlich bis ungefähr in die Gegend von Santa Cruz de la Sierra, noch umfasst, so dass also die umfangreichen Waldgebiete am Fusse der Kordillere auch noch zur amazonischen Hyläa zu rechnen sind. Auch die in Nordostbolivien sehr ausgeprägten Savannengebiete, wie ich sie z.B. am Rio Yacuma antraf, gehören noch zum Gebiet der Fauna der amazonischen Hyläa, d.h. die kleineren und grösseren Waldinseln dieser Savannen beherbergen eine mehr oder weniger verarmte Waldfauna. Auf dem Kamp zwischen den Waldinseln dagegen finden sich meist schon Arten südlicherer Herkunft Bei manchen weitverbreiteten Arten, wie z.B. bei *Papilio anchisiades*, die im amazonischen Gebiet in einer anderen Form auftreten als im Süden, findet sich hier im Gebiet der Savannen, noch ausgeprägter allerdings in der nächsten Zone, ein mehr oder weniger breiter Streifen, in dem je nach der betreffenden Art, die beiden Formen entweder nebenainander fliegen oder einen echten Übergang, einen Kline, bilden.

Als zweites der tiergeographischen Gebiete des Tieflandes greift von Osten, von Matto Grosso her die Fauna Zentralbrasiliens weit nach Bolivien hinein. Die Llanos de Mojos z.B. können noch als fast reines Gebiet dieser Fauna betrachtet werden. Die Kenntnisse bezüglich der Insektenfauna dieser abgelegenen Gegenden sind aber noch viel zu gering, um schon genaue Angaben machen zu können.

Das südostbolivianische Tief- und Hügelland von Chiquitos als drittes tiergeographisches Gebiet Boliviens gehört der Zusammensetzung seiner Fauna nach bereits eindeutig zum südlich angrenzenden Gebiet von Nordargentinien und Paraguay, das seine extreme Ausbildung in der Fauna des Gran Chaco findet. Zahlreiche Arten und Gattungen erreichen hier ihre Nordgrenze, wie z.B. *Graphium microdamus* Burm. oder die Arten der Syntomiden-Gattung *Eurota*. Von weiter verbreiteten Arten fliegt hier bereits fast ausnahmslos die südlich verbreitete Subspecies. In den Sierren von Chiquitos scheinen sich auch endemische Arten und Formen ausgebildet zu haben, doch ist bei der Feststellung von Endemismen in noch unzureichend erforschten Gebieten bekanntlich grösste Vorsicht geboten, weswegen ich weitergehende Schlüsse lieber noch unterlasse. Im Norden dieses Gebietes, gegen den Rio Grande zu, verläuft für viele Arten die oben schon erwähnte Nordgrenze, bzw. es beginnt das erwähnte Mischgebiet.

Im Norden, im Osten und im Süden von Ostbolivien sind die drei erwähnten Faunen, die amazonische, die zentralbrasilianische und die nordargentinische mehr oder weniger rein ausgebildet, der grösste Teil des bolivianischen Ostens bildet aber, wie ja aus meinen bisherigen Ausführungen bereits hervorging, ein Mischgebiet, in dem diese drei Faunen mehr oder weniger rasch ineinander übergehen. Das interessanteste Mischgebiet in dieser Hinsicht scheint das weitere Gebiet um Santa Cruz de la Sierra su sein, in das als vierte tiergeograhpische Komponente auch noch die Fauna des Osthanges der Kordillere, der Yungas einstrahlt.

Diese Fauna der Yungas, der Regenwälder am Ostabfall der Kordillere bis zu einer Höhe von gegen 3500m, dürfte wohl eine der interessantesten und wohl die artenreichste Südamerikas sein. Die Yungasfauna ist von Kolumbien bis zum Andenknie in der Höhe von Santa Cruz de la Sierra, also bis zum Ausklingen der tropischen Regenwälder in den

Höhentrufen zwischen 500 und 3500m recht einheitlich verbreitet. Sie umfasst eine grosse Anzahl nur ihr eigentümlicher Arten. Dabei ist auffällig, dass zwar die Zahl der Arten von Norden nach Süden abnimmt, die Unterschiede bezüglich der artlichen Zusammensetzung nach der Höhe zu aber wesentlich grösser sind, als die zwischen Nord und Süd. Typische Arten der Yungas sind z.B. *Papilio isidorus* Doubl. in der unteren Waldstufe, *Papilio warscewiczii* Hpffr. in der oberen, die Arten der Weisslinggattung *Catasticta* und die meisten *Dismorphia*-Arten. Diese Yungasfauna ist ihrer Enstehung nach, erdgeschichtlich gesehen, verhältnismässig jung. Erst die im jüngeren Tertiär erfolgte Hebung der Kordillere, die offensichtlich auch heute noch andauert, schuf die Vorbedingung für die Entstehung dieser tropischen Gebirgsfauna. Während im Tieflande die Lebensbedingungen sich mindestens seit dem mittleren Tertiär kaum änderten, von aussen her jedenfalls seit langer Zeit kaum ein Zwang zur Umbildung der vorhandenen Formen wirksam wurde, wurde die Fauna in den von der Auffaltung und Hebung betroffenen Gebieten gezwungen, sich entweder den veränderten Lebensbedingungen durch entsprechende Umwandlungen anzupassen oder aber zugrundezugehen. Dazu kamen noch im Gefolge der erdgeschichtlichen geologischen Vorgänge und sicherlich auch der eiszeitlichen Klimaschwankungen zeitweise Isolierungen grösserer oder kleinerer Populationen, was alles zusammen die Entstehung der heute so überaus mannigfaltigen Fauna der Yungas ermöglichte. Die Abstammung dieser Tierwelt der tropischen Bergwälder von der tertiären tropischen Tieflandfauna geht aus der nahen Verwandtschaft der Angehörigen der beiden Faunen klar hervor, während zur Fauna der Hochkordillere so gut wie keinerlei Beziehungen bestehen.

Diese Fauna des Hochlandes und des Hochgebirges, also der waldfreien Gebiete oberhalb der zwischen 3000 und 3500m verlaufenden Baumgrenze bildet gegenüber den bisher besprochenen Faunen eine Einheit, obgleich sie auch ihrerseits wieder in verschiedene, durch die Höhenlage bedingte Gebiete zerfällt. Im ganzen gesehen fällt auf, dass die Fauna dieser Gebiete seht wenig "südamerikanische" Elemente enthält, dagegen in der Hauptsache Gattungen, die vorzugsweise holarktisch verbreitet sind, wie z.B. die Gattung *Colias* oder die doch wenigstens ihre nächsten Verwandten in der Holarktis haben, wie die Weisslingsgattung *Phulia*, die zweifellos nächstverwandt zur zentralasiatischen Gattung *Baltia* ist. Die ursprünglich sicher auch hier heimische tropische Insektenfauna wurde im Laufe der Hebung des Landes seit dem Tertiär in den über der Baumgrenze gelegenen Teilen des Hochlandes offensichtlich vernichtet. Es darf in diesem Zusammenhange auch daran erinnert werden, dass bei Potosi in über 4000m Höhe eine tertiäre Flora fossil gefunden wurde, die mit Sicherheit einst in tieferen Lagen gediehen ist. Anstelle der untergegangenen Tieflandfauna wanderten von Norden her aus der gemässigten Zone stammende Formen ein und besiedelten die weiten Hochländer. Auf welchem Wege allerdings diese Einwanderung im Einzelnen vor sich ging, ist noch umstritten. Sicher dürfte aber sein, dass diese Einwanderung in mehreren Wellen erfolgte, von denen die letzte vermutlich erst nach der letzten Eiszeit anlangte. Auch die Wirkung der Eiszeiten ist aus dem derzeitigen Formenbestand der Fauna des Hochlandes zu erkennen, da ja angenommen werden muss, dass beim jeweiligen Höchststand der Vereisung die Formen, ähnlich wie in der Alten Welt, auf bestimmte Refugialgebiete zurückgedrängt wurden, in denen sich dann neue Formen ausbilden konnten. Allerdings vollzogen sich in Südamerika die Faunenverschiebungen infolge der Eiszeiten anscheinend nicht so weiträumig wie in der Alten Welt. Bestehende Gattungsdifferenzierungen, wie z.B. die der beiden Weisslingsgattungen *Phulia* und *Piercolias*, deren nächste Verwandte, wie schon erwähnt, im Pamir in Zentralasien leben, sind vermutlich Ergebnisse einer durch eine frühere Eiszeit bewirkten Isolierung. Die Aufspaltung der beiden gennanten Gattungen in zahlreiche, sich nahestehende Arten mit oft sehr begrenzten Verbreitungsgebieten dagegen dürfte erst im Verlauf der letzten Eiszeit erfolgt sein. Die in Eurasien und Nordamerika mit vielen Arten weitverbreitete Gattung *Colias* dagegen ist vermutlich erst in, erdgeschichtlich ganz junger Zeit, nach der letzten Vereisung eingewandert, denn die hochandinen Arten dieser Gattung sind noch kaum in konstante geographische Formen aufgespalten und zeigen noch in jeder Hinsicht grosse Ähnlichkeiten mit ihren Verwandten in der Holarktis.—Die Frage der Ähnlichkeit zwischen den südamerikanischen Hochlandindianern und den Bewohnern der Hochländer Zentralasiens, insbesondere Tibets, sei nur am Rande erwähnt, wobei an echte nähere Verwandtschaft oder aber an Konvergenzentwicklungen entfernt verwandter Gruppen infolge der Ähnlichkeit der Umwelteinflüsse gedacht werden kann.

Auch die Fauna des bolivianischen Hochlandes, in grossen Zügen zwar recht einheitlich, lässt doch gewisse Unterschiede in den verschiedenen Gegenden und Höhenlagen erkennen.

Die Hochgebirgsstufe der Ostkordillere von ca. 4600 bis über 5000m wird nur von wenigen an die extremen Verhältnisse dieser Stufe angepassten Arten bewohnt, wie *Piercolias andina* Stgr., *Phulia paranympha* Stgr. und *Argynnis inca* Stgr. Es sind dies Arten, die in den höchsten Lagen der Kordillere auch in Peru vorkommen. Andere Arten aus dem Altiplano und selbst aus tieferen Lagen der Yungas werden nicht allzuselten durch Luftströmungen in diese Höhen getragen und finden dann meist durch Erfrieren auf den Schneefeldern ihr Ende. Ebenso geht anscheinend ein Teil der Tiere zu Grunde, die als Wanderer aktiv die Kordillere überschreiten. Zu diesen Arten gehört u.a. *Colias euxanthe* Feld.

Die Fauna des eigentlichen Altiplano, des Hochlandes zwischen den Hochgebirgen in 4000-4600m Höhe ist bereits wesentlich reicher. Neben Arten, die für den Altiplano Boliviens und Perus charakteristisch sind, finden sich hier, namentlich im Südwesten und im Westen solche, die ihre Hauptverbreitung in Chile haben und dort im Süden des Landes bis auf Meereshöhe hinabsteigen. Hieher gehören u.a. verschiedene *Tatochila*-Arten. Die Westkordillere beherbergt eine Fauna, die noch nahezu völlig unbekannt ist. Die wenigen Proben lassen aber erkennen, dass nächste Beziehungen zur chilenischen Fauna bestehen.

In den in den Altiplano tiefer eingeschnittenen Tälern, z.B. im Tal von La Paz tritt eine wesentlich reichere Fauna auf, die aber zum grössten Teil immer noch aus Arten besteht, die nicht als eigentlich südamerikanisch zu bezeichnen sind. Arten, wie die Saturnide *Automeris stuarti* Rothsch. und einige andere sind allerdings bereits typische Vertreter der neotropischen Fauna, die durch die Flusstäler bis hierher vorgedrungen sind. Die Fauna der tiefen Durchbruchstäler des Rio La Paz und anderer Flüsse, die zu den trockensten und sterilsten Plätzen Boliviens gehören, ist noch nahezu unbekannt, dürfte aber nach den vorliegenden Proben stark verarmt sein und grosse Anklänge an die Fauna der Valles Südostboliviens zeigen.

Die Fauna der Ostseite der Kordillere über der Baumgrenze, also in den dort ausgebildeten oft recht üppigen Grasfluren zwischen 3500 und 4500m ist noch so gut wie unbekannt, dürfte aber nach meinen Fangergebnissen im oberen Songotal ebenfalls nahe Beziehungen zur holarktischen Fauna aufweisen.

Das letzte Gebiet, das südostbolivianische Bergland, ist entomologisch noch sehr wenig bekannt. Soweit das vorliegende Material und die Literaturangaben erkennen lassen, bildet es tiergeographisch eine Einheit mit Nordwestargentinien, den Gebirgen von Salta und Jujuy südlich etwa bis in die Gegend von Tucuman. In den Hochlagen finden sich hier noch typisch hochandine Formen, wie *Argynnis*- und *Phulia*-Arten. In den trockenen subtropischen innerandinen Tälern, den sogenannten Valles, aber eine recht eigentümliche nur hier und in Nordwestargentinien vorkommende altertümlich anmutende Fauna. Arten wie *Teriocolias atinas* Hew. und *Mathania carrizoi* Giac. scheinen für diese Valles charakteristisch zu sein und treten im Norden Boliviens nur in den heissen trockenen Durchbruchstälern der Flüsse, wie schon erwähnt, auf.

Die eben vorgenommene Einteilung Boliviens in tiergeographische Gebiete ist nur als ein vorläufiger Versuch zu werten und wird noch manche Änderung erfahren müssen, wenn einmal unsere Kenntnisse der so überaus interessanten Fauna Boliviens grösser geworden sind. Ich halte es aber doch für gut, diesen Entwurf einmal zur Diskussion zu stellen. Vielleicht haben andere Kollegen bei der Bearbeitung anderer Tiergruppen aus Bolivien ähnliche oder auch andere Erfahrungen gewonnen und ich wäre dankbar um Mitteilung derartiger Etgebnisse.

Section

on

PALAEONTOLOGY

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Section Editor

J. R. VOCKEROTH

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The following paper was presented at the Congress but is not included herein:

Recent Advances in our Knowledge of the Geological History of Insects

By F. M. CARPENTER

Harvard University

Cambridge, Mass.

The Cretaceous Caddisfly, *Dolophilus praemissus* Cockerell

By H. H. Ross
Illinois Natural History Survey
Urbana, Ill.

ABSTRACT

The fossil Dolophilus praemissus *Cockerell, described from Cretaceous Amber from eastern Tennessee, is represented only by the apical portion of the front wing. A study of this wing indicates that the species probably represents a primitive form of the family* Philopotamidae, *possibly near the existing genus* Sortosa; *there is a possibility, however, that the fossil may represent a primitive genus of the Psychomyiidae, possibly close to the existing genus* Phylocentropus. *The details of the head and legs will be necessary to achieve a more accurate placement. Whichever of these two placements is correct, this fossil would appear to give excellent evidence that a primitive member of one of these families occurred in this area during Cretaceous. The two genera which this fossil resembles,* Sortosa *and* Phylocentropus, *are cool-adapted groups which occur today in the mountains of eastern North America. Since the fossil under discussion is remarkably similar to these two genera in venation, it is quite possible that it was equally similar ecologically. This set of circumstances suggests the possibility that both cool-adapted caddisflies and montane stream conditions have been present continuously in eastern North America since Cretaceous times.*

DISCUSSION

Henry Dybas. What is known of the caddisflies in Baltic Amber and how do these Cretaceous fossils fit in with them?

H. H. Ross. Many species are known and these in the main represent modern genera.

W. L. Brown, Jr. 1. Where are Baltic Amber Trichopteran genera found living now? 2. The pattern you outline is similar to that of ants, the best known amber group.

H. H. Ross. 1. In total, in almost all parts of the world. Certain genera are now restricted to Europe, others (especially in the Psychomyiidae) are either holarctic or worldwide.

Ashley B. Gurney. Is the Canadian specimen to which reference was made represented by body parts as well as wings?

H. H. Ross. It has many body parts which may ultimately permit its accurate placement phylogenetically.

Cretaceous and Tertiary Insects in Arctic and Mexican Amber

By Paul D. Hurd, Jr., Ray F. Smith and Robert L. Usinger
University of California
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Since earliest times Baltic amber has overshadowed all other types of fossil resins because of its accessibility and abundance. Indeed, the name "amber" has become almost synonymous with succinite of the Baltic. However, other sources of amber are known, including Burma, Zanzibar, and the East Indies. In fact, fragmentary records appear in the literature from almost all parts of the world and it now appears that amber may be found almost any place where lignitic deposits occur. Most amber that has been studied scientifically is of Tertiary age, mostly from Eocene to Miocene, but some twenty years ago an important discovery was made (Carpenter, *et al.*, 1936, University of Toronto Studies, Geological Series No. 40) of Canadian amber of Cretaceous age. This important step opened new vistas in Paleoentomology, for the Cretaceous was a period of far greater significance than the Tertiary in the evolution of insects.

It is now possible, as a result of investigations at the University of California, to report the development of two additional sources of amber, one of Cretaceous age on the slopes of the Arctic Ocean near Pt. Barrow, and the other of Oligocene and Miocene age in Southern Mexico. Although it is too early to report in detail on the inclusions and no generalizations can be made until systematic studies are completed, it nevertheless seems appropriate to give some details on the current status of these two projects.

The Arctic amber occurs in shales exposed along the Colville River and in lignite beds along the upper reaches of the Kuk River south of Wainwright. These beds are clearly of Cretaceous age and field work is being carried out at the present time to determine whether they are Lower Cretaceous or Upper Cretaceous. Although the Arctic amber can be found in place, it is collected in greater quantities and in better condition in beach drift, especially along the shores of the Kuk River near the mouths of the Omalik, Avalik and Ketik Rivers. Thousands of pieces, mostly of small size, are now available from this source and work is progressing on the examination of individual pieces for the presence of inclusions. Thus far only three kinds of insects have been found: one a small Empidid? fly, another a new genus and species of Eulophidae (Chalcidoidea) and third, an Adelgid. Several specimens of the Eulophid and Adelgid occur. The Arctic field work has been supported by the Arctic Institute of North America under a contract with the Office of Naval Research.

Mexican amber has been collected largely through the interest and generous assistance of Mr. and Mrs. Franz Blom of San Cristobal de las Casas, Chiapas, Mexico. Amber has long been known in the form of articles of jewelry on the Indians of Chiapas. The source was recognized as areas exposed by the river in the vicinity of Simajovel, but no one had collected the amber for scientific purposes. Several years ago the Associates in Tropical Biogeography of the University of California undertook a program of financial support for investigation of Mexican amber. Several trips have been made to the area and, with the aid of the Bloms, a sizable collection has been accumulated including insects of about 75 species representing all of the major orders. The amber has been positively dated as Oligocene and Miocene with the possibility of material in some areas from the Eocene epoch.

The following scientists have participated in the amber projects: Advisory and administrative—G. Dallas Hanna, E. Gorton Linsley, R. A. Stirton; Arctic amber—R. L. Langenheim, C. J. Smiley, R. F. Smith, R. L. Usinger; Mexican Amber—J. Wyatt Durham, E. E. Gilbert, P. D. Hurd, C. D. MacNeill and R. F. Smith.

Les Insectes Paléozoïques du Sud de la Sibérie[1]

Par B. B. Rohdendorf
Institut Paléontologique de l'Académie des Sciences de l'URSS
Moscou, U.R.S.S.

L'étude des restes d'insectes, trouvés dans les dépôts paléozoïques du sud de la Sibérie dans la région du bassin de Kuznetsk (Kousbass), a permis d'éclaircir certaines des particularités de la faune du continent paléozoïque de l'Angaride. Jusqu'en ces dernières années, les insectes paléozoïques de l'Asie n'étaient connus que par des exemplaires isolés et trouvés par hasard, en Sibérie, en Extrême-Orient et aux Indes. Les études paléozoïques récemment effectuées à l'Institut Paléontologique des dépôts continentaux, ont changé la situation, en faisant connaître la composition riche et particulière de cette faune.

Les gisements découverts et étudiés, contenant des restes d'insectes du paléozoïque, sont situés dans la région de Kemerovo, aux bords de la rivière Tome et de ses affluents. Actuellement, on a découvert plus de 25 gisements d'insectes du carbonifère et du permien. Ces gisements éclairent la faune de diverses parties des sédiments houillers du bassin, en commençant par la suite Balakhonienne, la plus ancienne, jusqu'à l'Erounakovienne, la plus jeune. Toutes ces données réunies permettent de juger des vraies particularités de la faune et de ses changements durant un temps géologique relativement très long. L'importance des matériaux d'insectes fossiles provenant du sud de la Sibérie est encore plus considérable, si nous rappelons qu'il existait déjà certains renseignements sur des faunes plus récentes des périodes du Triassique et du Jurassique, dont les gisements sont encore peu étudiés. Une grande quantité d'échantillons paléontologiques embrassant la période du Carbonifère jusqu'à la moitié de l'ère du Mésozoïque et provenant d'un territoire fort limité, est aussi fort intéressante et n'a pas d'égal dans d'autres régions.

Dans les dépôts paléozoïques du bassin de Kuznetsk, on a trouvé près de 4500 échantillons dont la distribution entre les divers gisements est incomparable. La majorité de ces échantilllons représente des découvertes isolées, mais certains gisements ont donné un grand nombre de restes fossiles; ces riches collections sont d'une grande importance et permettent de caractériser plus adéquatement la composition du complexe faunistique.

Les plus vastes collections proviennent du Kaltan. Ce gisement a fourni près de 2000 échantillons d'insectes du Permien inférieur. Beaucoup d'insectes ont également été recueillis dans les dépôts permiens plus jeunes provenant des suites Iljinskienne et Erounakovienne, tels les gisements Surijokovo (Souryokovo, 700 échantillons) et Sokolovo (650 échantillons). Le gisement Zhelty Jar (Gelty Yar), de la suite Balakhonienne, la plus ancienne datant de la période du Carbonifère, a aussi fourni une riche collection ne comptant pas moins de 750 échantillons.

La détermination des insectes fossiles a été faite par des entomologistes spécialisés dans l'étude de la phylogénèse et la systématique des ordres ou des divers groupes d'insectes. Les Homoptères et les Psocoptères ont été décrits par E. E. Becker-Migisova; les Mecopteroidea, Neuroptera et certains Orthopteroidea (Glosselytrodea, Miomoptera) par O. M. Martynova; les Palaeodictyoptera, Megasecoptera, Diaphanopterodea, Odonata et Coleoptera par B. B. Rohdendorf. Enfin les quelques espèces diverses ont été décrites par G. M. Zalessky. Les résultats des recherches de ces entomologistes ont servi à préparer cet aperçu. Ces données nous font voir que la composition de la faune paléozoïque des Insectes est très vaste. Les 261 espèces décrites représentent 12 ordres, 39 familles et 109 genres. Leur distribution selon les ordres et les complexes faunistiques de divers âges est donnée dans le tableau sur la page suivante.

De plus, il faut noter que l'étude du matériel d'Orthopteroidea n'est pas encore achevée. Ces insectes existent en nombres considérables dans les gisements Balakhonien et Kuznetskien, deux suites anciennes. C'est pourquoi le nombre total des espèces dans toute la collection paléozoïque pourra atteindre à peu près 300 espèces.

Le groupe varié des Palaeoptera, généralement bien représenté dans les faunes paléozoïques, est pauvre en espèces dans le matériel Sibérien provenant des suites Balakhonienne et Kuznetskienne, c'est à dire des dépôts du Carbonifère supérieur et du Permien inférieur.

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[1] Ce travail a déjà été publié en langue russe, accompagné d'un résumé en français par le même auteur, dans *Revue d'entomologie de l'URSS* 35 (3): 611–619, 1956. Prière de référer à cette publication qui contient une bibliographie et des figures additionnelles.

Nombre d'insectes du paléozoïque de Kouzbass étudiés.

Ordres	Nombre par catégorie			Nombre d'espèces dans chaque suite			
	familles	genres	espèces	Balakhonienne	Kuznetskienne	Iljnskienne	Erunakovienne
Palaeodictyoptera	2	3	3	3	–	–	–
Megasecoptera	1	1	1	1	–	–	–
Diaphanopterodea	3	4	6	2	4	–	–
Odonata	2	2	2	–	2	–	–
Glosselytrodea	3	5	13	–	7	5	1
Miomoptera	2	3	5	–	2	2	1
Homoptera	23	41	68	2	40	15	11
Psocoptera	2	5	9	–	2	7	–
Neuroptera	1	1	1	–	–	–	1
Trichoptera	1	1	1	–	1	–	–
Mecoptera	6	17	98	–	51	33	14
Coleoptera	3	26	55	–	6	16	33
Total:	38	109	262	8	115	78	61

Vaste et bien représenté dans tous les complexes faunistiques du Carbonifère connus jusqu'ici et dans certains du Permien inférieur, l'ordre des Palaeodictyoptera est fort pauvrement representé en Sibérie, au paléozoïque. Seulement 3 genres appartenant à deux familles et provenant de la suite Balakhonienne, ont été décrits. La famille Dictyoneuridae, connue jusqu'ici par plusieurs de ses genres provenant du Carbonifère supérieur et moyen de l'Europe et de l'Amérique du Nord, est représentée par un nouveau genre particulier, trouvé au bas de la suite Balakhonienne. Une autre famille était déjà connue des dépôts du Carbonifère supérieur et du Permien inférieur.

Le seul représentant des Megasecoptera, provenant de la suite Balakhonienne, est le deuxième genre de la famille des Vorkutiidae récemment décrite d'après des échantillons en provenance des dépôts du Permien inférieur du nord de l'Ural.

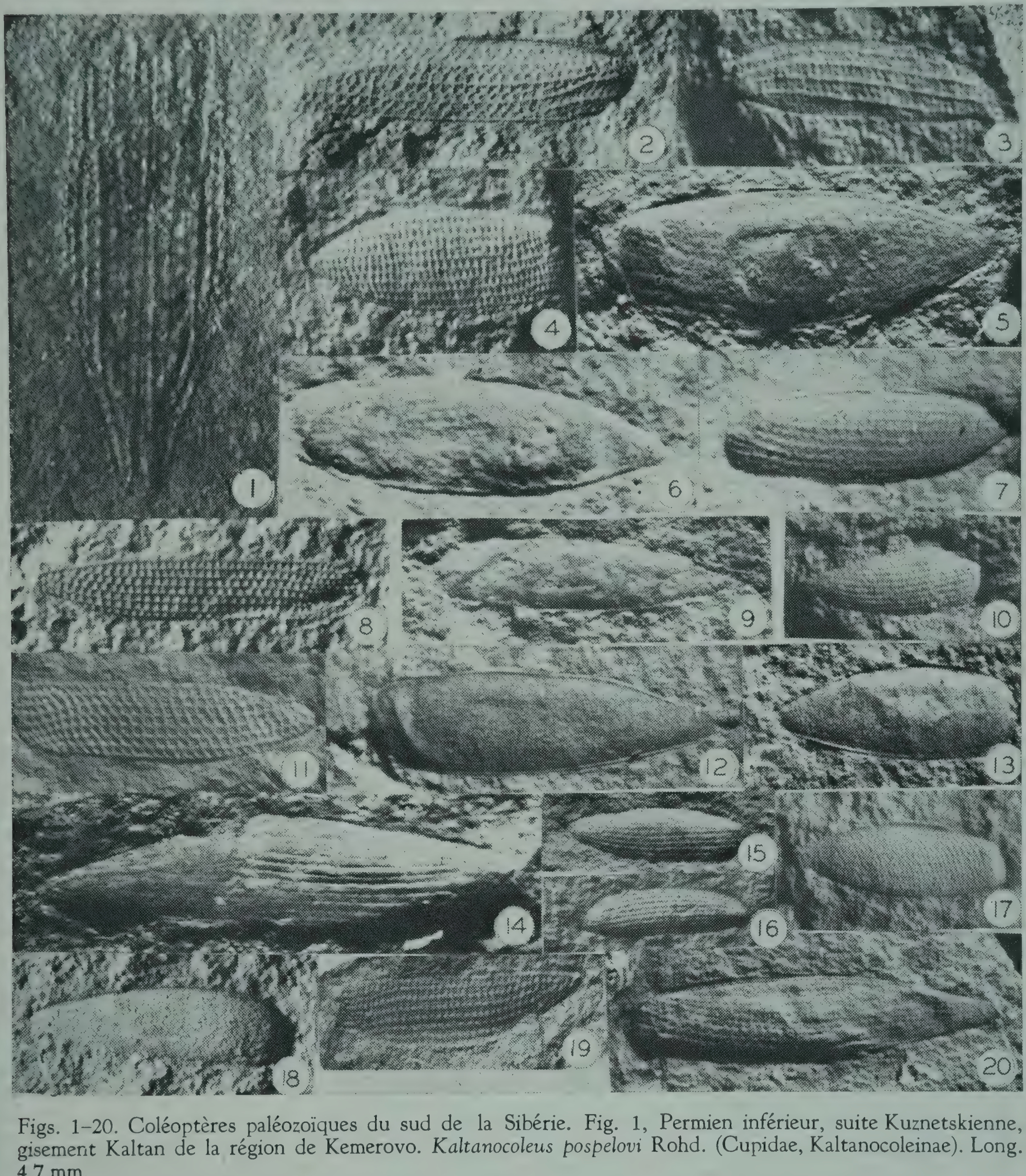
Les plus nombreux Palaeoptera, soit les espèces de l'ordre des Diaphanopterodea, appartiennent à ses trois familles. L'une d'elles n'était connue jusqu'ici que par des spécimens du Carbonifère supérieur de l'Europe (Diaphanopteridae), et les deux autres ont été décrites récemment de la suite Kuznetskienne.

L'ordre considérable et aux espèces variées des Odonates n'a fourni que deux genres provenant de deux familles, dans la suite Kuznetskienne: une des familles, celle des Kennedyidae était déjà connue du Permien inférieur de l'Amérique; l'autre est nouvelle et forme un genre très rapproché des espèces du Permien inférieur.

Tous les autres insectes paléozoïques du bassin de Kuznetsk appartiennent à huit ordres des Neoptera et composent la majorité des espèces.

Les deux premiers ordres des Neoptera appartiennent au groupe Orthopteroidea. L'ordre des Miomoptera se rencontre dans chacune des trois suites permiennes et comprend des espèces appartenant à deux familles. Quatre espèces de la famille des Delopteridae, connue auparavant, ont été trouvées dans les suites Kuznetskienne et Iljinskienne. La deuxième famille, celle des Archaemiopteridae, était connue jusqu'ici seulement dans les dépôts stéphaniens du Carbonifère de l'Europe; au bassin de Kuznetsk, cette famille est représentée dans les dépôts Erunakoviens (Permien supérieur) par un nouveau genre. Les autres Orthoptéroïdes sont plus variés; ce sont des espèces de l'ordre des Glosselytrodea décrits jusqu'à maintenant du Permien supérieur et du Triassique seulement. Ici, ces insectes sont représentés par 13 espèces, cinq genres, trois familles, presque toutes ces formes étant trouvées pour la première fois. La famille de Eoglosselytridae, contenant les premiers Glosselytrodes du Permien inférieur, à caractères très primitifs est d'un intérêt particulier; ses 11 espèces réparties en 3 genres, ont été décrites de la suite Kuznetskienne. La découverte du genre *Permoberotha* Till., de la famille correspondante, connue jusqu'ici seulement du Permien inférieur de l'Amérique, est un fait important.

L'ordre des Homoptères occupe une des premières places dans la faune par la diversité et le nombre de ses espèces; des fossiles ont été découverts dans les dépôts de toutes les suites paléozoïques de la masse houillère. De la suite Balakhonienne, la plus ancienne du Carbonifère, proviennent seulement deux espèces d'Homoptères, dont l'une est surtout intéressante parce qu'elle montre toute une série de caractères analogues aux Blattodea. Cette forme, *Blattoprosbole tomiensis* B.-M., appartient à une famille particulière, les



Figs. 1–20. Coléoptères paléozoïques du sud de la Sibérie. Fig. 1, Permien inférieur, suite Kuznetskienne, gisement Kaltan de la région de Kemerovo. *Kaltanocoleus pospelovi* Rohd. (Cupidae, Kaltanocoleinae). Long. 4,7 mm.

Figs. 2–20, Permien supérieur, suite Erunakovienne, gisement Sokolova de la région de Kemerovo. 2, *Permocupoides skoki* Rohd. (Cupidae s.str.). Long. 5,0 mm. 3, *Tomiocupes carinatus* Rohd. (Cupidae s.str.). Long. 3,0 mm. 4, *Taldycupes moltshanovi* Rohd. (Cupidae, Taldycupinae). Long. 2,6 mm. 5, *Karakanocoleodes latissimus* Rohd. (Curculiopseidae). Long. 4,4 mm. 6, *Karakanocoleus major* Rohd. (Curculiopseidae). Long. 4,6 mm. 7, *Taldycupes khalfini* Rohd. (Cupidae, Taldycupinae). Long. 2,9 mm. 8, *Tychticupes vasjuchitshevi* Rohd. (Cupidae, Taldycupinae). Long. 3,4 mm. 9, *Uskatocoleus angustior* Rohd. (Curculiopseidae). Long. 3,15 mm. 10, *Ademosyne sibirica* Rohd. (Permosynidae). Long. 1,7 mm. 11, *Tychticupes ragozini* Rohd. (Cupidae, Taldycupinae). Long. 3,0 mm. 12, *Uskatocoleus zalesskyi* Rohd. (Curculiopseidae). Long. 3,5 mm. 13, *Uskatocoleus lutugini* Rohd. (Curculiopseidae). Long. 2,35 mm. 14, *Rhombocoleus andreae* Rohd. (Cupidae, Rhombocoleinae). Long. 4,8 mm. 15, *Ademosyne neuburgae* Rohd. (Permosynidae). Long. 1,8 mm. 16, *Uskaticupes fomitshevi* Rohd. (Cupidae, Taldycupinae). Long. 1,8 mm. 17, *Taldycupidium bergi* Rohd. (Cupidae, Taldycupinae). Long 2,1 mm. 18, *Karakanocoleus lebedevi* Rohd. (Curculiopseidae). Long. 2,7 mm. 19, *Tychticupes radtshenkoi* Rohd. (Cupidae, Taldycupinae). Long. 2,5 mm. 20, *Erunakicupes angustus* Rohd. (Cupidae, Rhombocoleinae). Long. 4,0 mm.

Blattoprosbolidae B. M. qui est très proche d'une famille récemment décrite du Namurien de l'Europe occidentale.

La majorité des Homoptères que l'on connaît aujourd'hui est représentée par des familles et des genres représentant les faunes paléozoïques et, en premier lieu, celle du Permien. Telles sont les sept familles suivantes, presque exceptionnellement permiennes: Prosbolidae, Scytinopteridae, Pereboridae, Archaescytinidae, Cicadopsyllidae, Protopsyllidiidae et Permaleurodidae. Ces familles paléozoïques réunissent 30 genres, c'est-à-dire les ¾ de tous les Homoptères. Les deux premières familles sont surtout bien représentées et contiennent 46 espèces et 18 genres, c'est-à-dire les ⅔ de toutes les espèces d'Homoptères de cette collection.

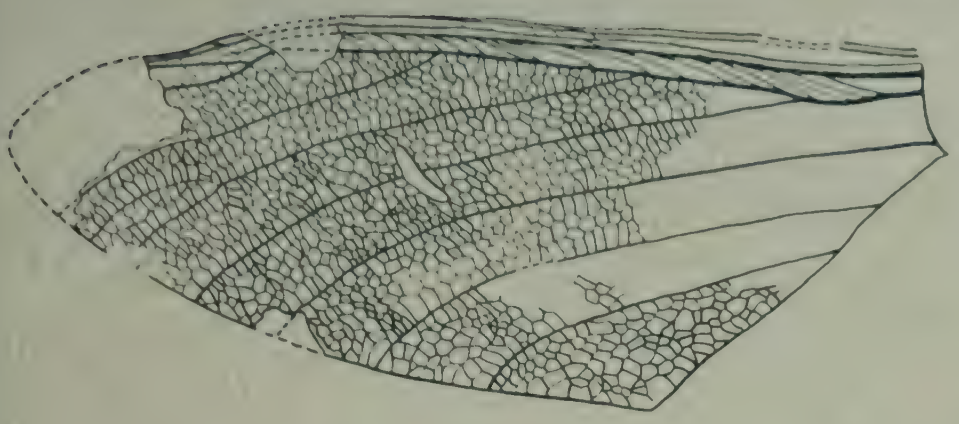
Cinq familles d'Homoptères découverts au Paléozoïque, dans le bassin de Kuznetsk, se rencontrent dans des faunes plus jeunes—du Triassique (Dunstaniidae, Ipsviciidae, Uninervidae) ou même dans les faunes tertiaires et modernes (Fulgoridae et Cixiidae). Mais le nombre des genres et des espèces de ces cinq familles, reliant notre faune avec les plus jeunes, n'est relativement pas grand, soit seulement 10. Ce qui caractérise les Homoptères du Paléozoïque c'est la présence de plusieurs genres endémiques, dont le nombre atteint 30, ce qui constitue les ¾ des tous les Homoptères. La majeure partie des familles est composée exceptionnellement de genres endémiques, trouvés seulement dans le sud de la Sibérie; dans d'autres familles, telles que les Prosbolidae, Scytinopteridae et Cixiidae, les genres endémiques prédominent fortement sur les autres. C'est seulement dans les deux familles des Archaescytinidae et les Cicadopsyllidae que les espèces endémiques présentent une minorité. Ainsi, bien qu'on n'ait pas trouvé parmi les Homoptères de la Sibérie des familles endémiques, l'endémisme générale est très considérable.

En conclusion, il me faut citer deux familles particulières qui présentent un grand intérêt phylogénétique, soit les Protopsyllidiidae, que l'on croît être les ancêtres des Coccodea modernes et la famille fort spécialisée des Uninervidae, probablement liée à certains groupes régressifs d'insectes parasitiques du Cénozoïque.

Voisin des Homoptères se trouve l'ordre des Psocoptères, qui réunit neuf espèces appartenant à cinq genres et aux deux familles Lophioneuridae et Surijokopsocidae B.-M. La première famille est largement distribuée au Permien en Amérique et en Australie, la seconde est endémique en Sibérie et connue par une seule espèce et un seul genre. La composition de la première famille montre aussi une grande originalité de la faune sibérienne: des quatre genres représentés, trois sont endémiques et seulement le genre *Zoropsocus* Tillyard est largement distribué. La famille endémique appelée Surijokopsocidae, se caractérise par certains traits progressifs de la morphologie des ailes.

L'ordre de Trichoptères est représenté par une seule forme trouvée dans le gisement du Permien inférieur de la suite Kuznetskienne. Cette trouvaille est d'un grand intérêt, puisqu'elle montre l'ancienneté de ces insectes, connus jusqu'ici seulement au Jurassique. La morphologie de cette forme est particulière ayant, à côté de caractères primitifs, des indices de haute spécialisation.

Fig. 21, *Asiodictya rossica* Rohd. (Palaeodictyoptera, Dictyoneuridae). Carbonifère supérieur, suite Balakhonienne, gisement Zavjalovo (région de Novosibirsk): aile (longueur 65 mm.) et portion de l'aile (grossissement 12). Fig. 22, *Callimokaltania martynovi* G. Zal. (Odonata, Protanisoptera, Callimokaltaniidae): Permien inférieur, suite Kuznetskienne, gis. Kaltan (région de Kemerovo); aile (long. 28 mm.). Fig. 23, *Aenigmatidia kaltanica* Rohd. (Diaphanopterodea, Aenigmatidiidae): Permien inférieur, suite Kuznetskienne, gis. Kaltan (région de Kemerovo): aile (long. 3,75 mm.). Fig. 24, *Kaltanoneura martynovi* Rohd. (Odonata, Zygoptera, Kennedyidae): Permien inférieur, suite Kusnetskienne, gis. Kaltan (région de Kemerovo); aile (long. 20 mm.). Fig. 25, *Siberiohymen asiaticus* Rohd. (Megasecoptera, Vorkutiidae): Carbonifère supérieur, suite Balakhonienne, gis. Verchotomskoje (région de Kemerovo); aile (long. 17 mm.). Fig. 26, *Permocupoides skoki* Rohd. (Coleoptera, Cupidae): Permien supérieur, suite Erunakovienne, gis. Sokolova (région de Kemerovo) ; élytre (long. 5 mm.). Fig. 27, *Tomiocupes carinatus* Rohd. (Coleoptera, Cupidae): Permien supérieur, suite Erunakovienne, gis. Sokolova (région de Kemerovo); élytre (long. 3 mm.). Fig. 28, *Protocupes martynovi* Rohd. (Coleoptera, Cupidae): Permien inférieur, suite Kusnetskienne, gis. Kaltan (région de Kemerovo); élytre (long. 3,5 mm.). Fig. 29, *Taldycupidium bergi* Rohd. (Coleoptera, Cupidae): Permien supérieur, suite Erunakovienne, gis. Sokolova (région de Kemerovo): élytre (long. 2,1 mm.). Fig. 30, *Schizocupes vetustus* Rohd. (Coleoptera, Curculiopseidae): Permien supérieur, suite Iljinskienne, gisement Surijokovo (région de Kemerovo); sculpture de la surface de l'élytre (grossissement 196). Fig. 31, *Curculiopsis grandis* Rohd. (Coleoptera, Curculiopseidae): Permien supérieur, suite Iljinskienne, gis. Surijokovo (région de Kemerovo); sculpture de la surface de l'élytre (grossissement 180).



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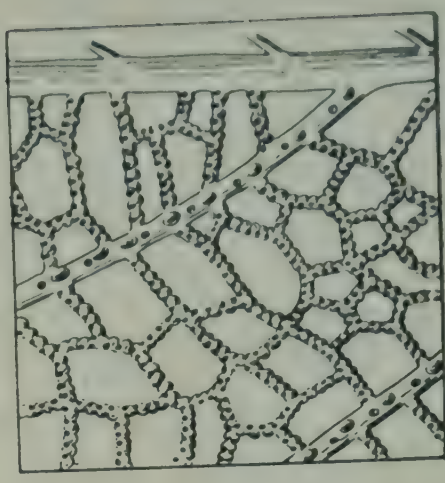

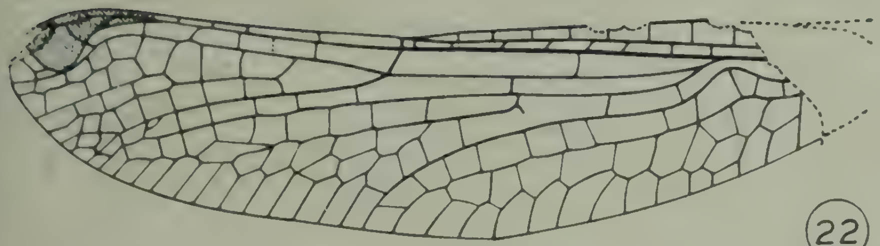

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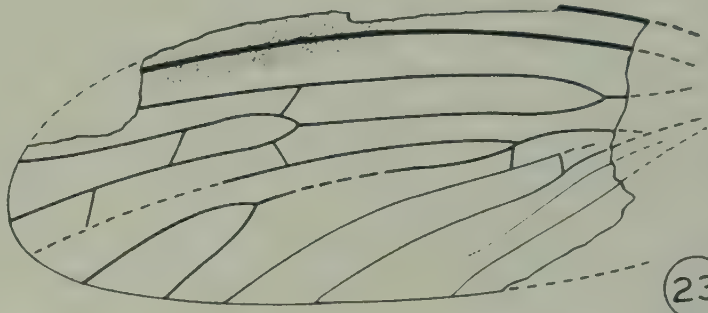

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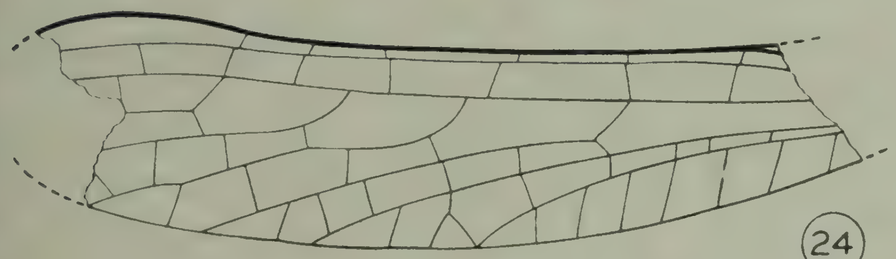

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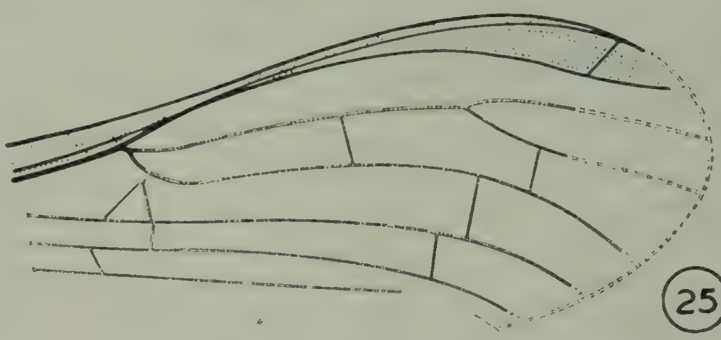

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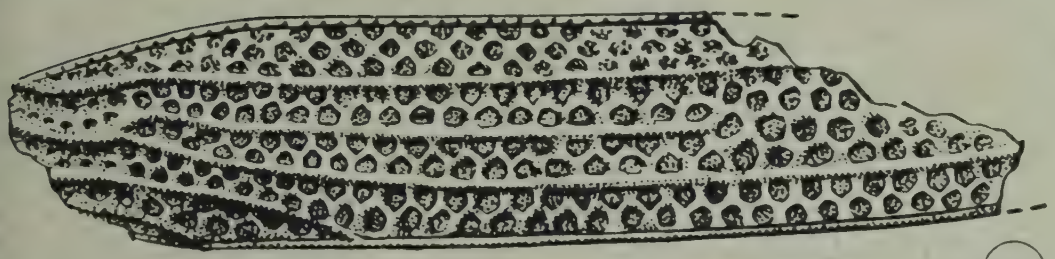

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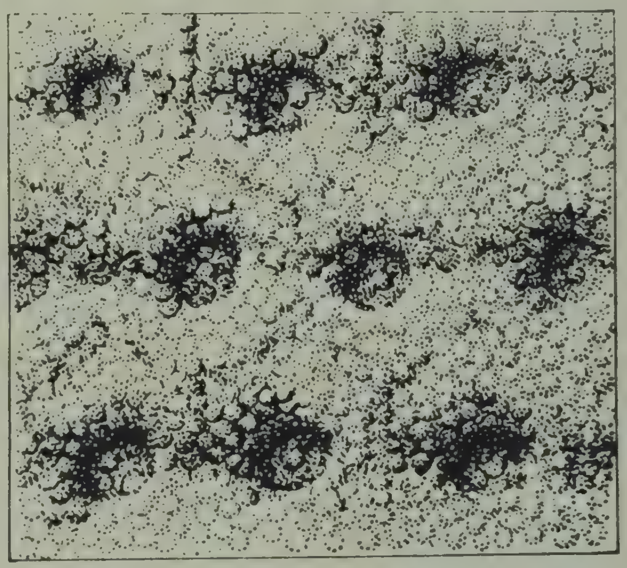

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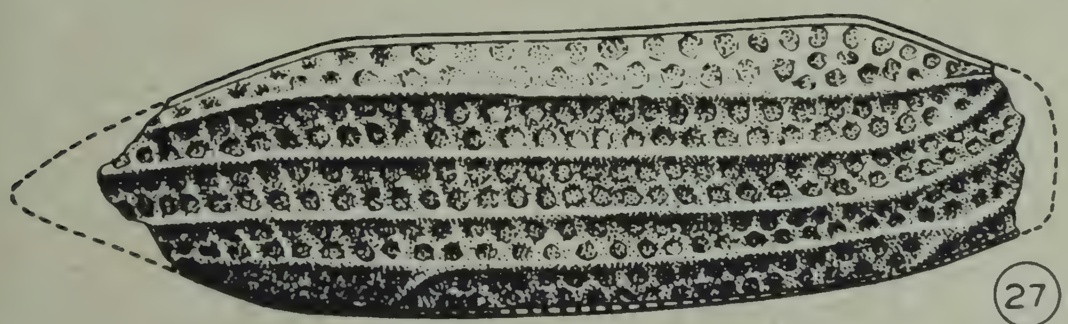

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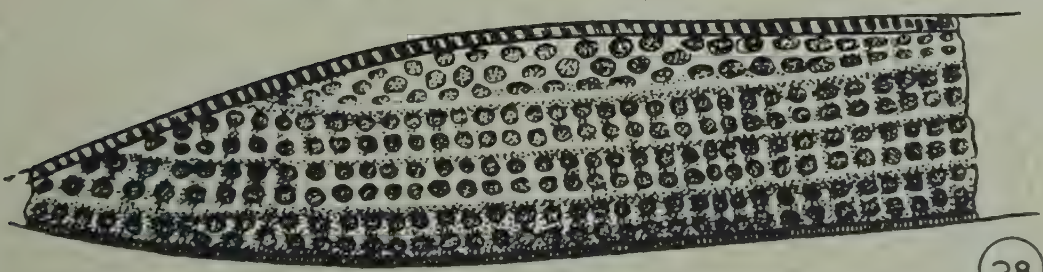

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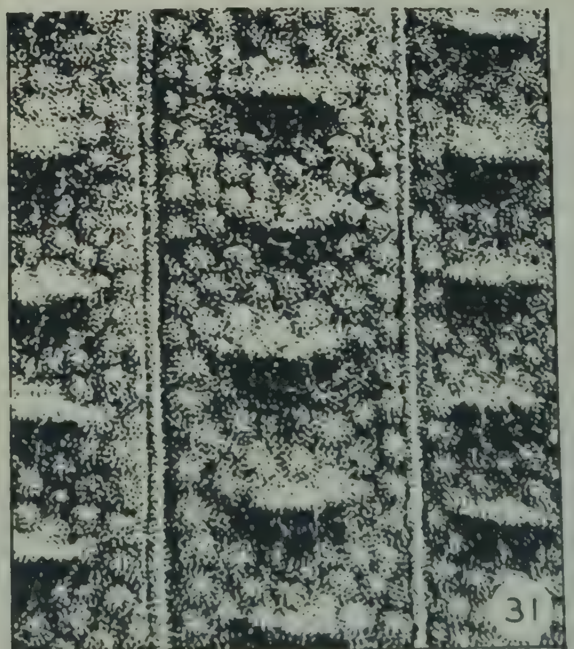

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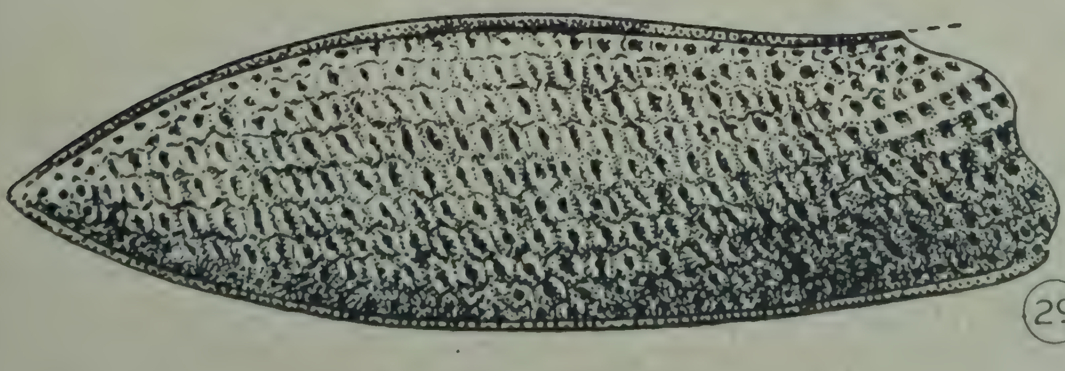

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L'ordre des Mécoptères est celui qui est le mieux représenté au Paléozoique par des échantillons du sud de la Sibérie. On a déjà décrit des dépôts permiens de Kouzbass près de 100 espèces comprises dans 17 genres et appartenant à six familles différentes. Les fossiles des Mécoptères sont trouvés dans toutes les suites de la masse houillère, excepté dans la Balakhonienne, la plus ancienne. Ce qui est le plus intéressant dans la distribution et la composition de cet ordre, c'est l'abondance inattendue des représentants du sous-ordre particulier des Protomécoptères, connu jusqu'ici seulement par des espèces appartenant à quatre genres et trois familles et provenant de l'Amérique et de l'Australie. Dans la Sibérie, on a découvert 27 espèces classées dans 7 genres et 4 familles, toutes, sans exception, étant nouvelles, et probablement des formes endémiques dans l'Angaride. Une telle abondance de Protomécoptères est très remarquable et fait voir les traits tout-à-fait particuliers de ce complexe faunistique.

L'autre particularité des Mécoptères du sud de la Sibérie est le grand nombre d'espèces appartenant à la famille des Permochoristidae, soit près de 70, classées en 9 genres, dont quatre sont endémiques. La deuxième famille, celle des Tychtopsychidae O. Mart., consiste en un seul genre ne contenant qu'une seule espèce qui a été trouvée dans les dépôts du Permien supérieur de la suite Erunakovienne du bassin de Kuznetsk.

En notant une grande originalité des Mécoptères paléozoïques de la Sibérie, exprimée dans l'endémisme non seulement de la majeure partie des genres, mais aussi dans la particularité des familles, il faut mentionner aussi une particularité curieuse de plusieurs représentants des Mécoptères sibériens, qui consiste dans la présence de poils sur les ailes, indiquée par des tubercules bien conservés sur les nervures, avec traces de fixation des poils. Tous les Mécoptères du Bassin de Kuznetsk sont tout-à-fait originaux, ce qui caractérise bien les complexes faunistiques de ces trois suites.

Les Coléoptères découverts dans toutes les suites permiennes du Kuzbass sont exceptionnellement variés, ce qui change complètement les notions sur les Coléoptères permiens, à l'effet que ce sont des formes peu nombreuses, fort isolées et rares. On a enregistré dans le Permien de la Sibérie, 55 espèces et 26 genres appartenant à au moins trois familles différentes; ces nombres indiquent bien clairement que les Coléoptères étaient abondants pendant le Permien sur le territoire d'Angaride, ce qui distingue bien cette région des autres.

La composition systématique et la distribution des Coléoptères parmi les complexes faunistiques des divers âges, permet de faire des conclusions significatives. Ce qui frappe d'abord, c'est l'augmentation régulière du nombre d'espèces et de genres de Coléoptères, à partir du complexe Kuznetskien, le plus ancien (6 espèces, 6 genres et 2 familles) en allant au Iljinskien (16 espèces, 10 genres et 2 familles) et jusqu'au Erunakovien (Permien supérieur) avec 33 espèces, 16 genres et 3 familles. Cette impression sommaire de croissance en nombres de la faune des Coléoptères pendant le temps du Permien sur le territoire du sud de la Sibérie, semble bien refléter l'histoire réelle de l'ordre des Coléoptères.

La composition systématique des Coléoptères permiens de la Sibérie attire une attention particulière. En soulignant l'endémisme extrême de toute la faune contenant 26 genres et 75 espèces, dont 20 genres et tous espèces sont nouveaux et proviennent du sud de la Sibérie, il faut remarquer les grandes difficultés dans l'éclaircissement des particularités et des rapports réciproques des familles des Coléoptères du Permien. La collection actuelle des Coléoptères fossiles (dont les restes consistent d'élytres isolés, plus rarement d'insectes entiers, privés presque toujours de pattes et d'antennes) ne permet pas d'éclaircir les principaux traits morphologiques caractérisant les grandes catégories systématiques de cet ordre d'insectes, comme la famille. C'est pourquoi nous sommes obligés de distribuer avec grande précaution les genres de Coléoptères permiens parmi les familles, évitant la description de groupements non complètement caractérisés.

L'abondance des espèces de la famille Cupidae, dont les représentants sont trouvés dans les dépôts de toutes les suites permiennes, est très caractéristique. Cette famille comprend 17 genres avec 28 espèces, qui forment quelques sous-familles. Parmi ces sous-familles, celle des Kaltanocoleinae primitifs est composée d'un seul genre et une seule espèce du complexe Kuznetskien; celle des Cupinae proprement dits comprend 6 genres distribués dans toutes les suites permiennes; enfin, celle des Taldycupinae, la plus riche en genres et en espèces, se compose de 8 genres et 16 espèces qui se trouvent également dans toutes les suites et montrent une plus grande diversité dans les dépôts Erunakoviens (Permien supérieur). La dernière sous-famille et la plus spécialisée, celle des Rhombocoleinae, qui contient deux genres et quatre espèces, a été découverte dans la suite Erunakovienne.

La deuxième famille, d'après l'abondance, celle des Curculiopseidae Mart. (6 genres, 23 espèces), est représentée aussi dans toutes les suites du Permien, mais par un seul exemplaire dans le complexe Kuznetskien (gis. Kaltan). L'endémisme de cette famille est relativement moins riches—ses deux genres ont été trouvés au Permien supérieur dans l'Oural et l'Australie (*Curculiopsis* Mart. et *Karakanocoleus* Rohd.). Dans la définition des traits caractéristiques de la structure des élytres des représentants des Curculiopseidae, on note une sous-estimation de certaines particularités structurelles. Ainsi, une des espèces du genre *Karakanocoleus* Rohd., avait déjà été étudiée par R. J. Tillyard et placée dans le genre *Permosyne* Till. (*P. pincombeae* Till., 1924), avec comme caractère important celui qui distingue les Curculiopseidae, c'est-a-dire cavité ou fente longitudinale. Un cas analogue a résulté de la description du type du genre *Curculiopsis* (*C. ellipticus* Mart., 1937), par A. V. Martynov. Bien que la cavité longitudinale fut bien marquée sur le fossile et même figurât sur le dessin, elle n'avait pas été considérée ou mentionnée dans la description. En effet, cette cavité longitudinale particulière est le caractère important de ces Coléoptères et se rencontre toujours sur les élytres des représentants de toutes les espèces de la famille, à un degré plus ou moins prononcé.

La dernière famille des Coleoptères fut découverte seulement dans les dépôts du Permien supérieur de la suite Erunakovienne. C'est celle des Permosynidae Tillyard, qui comprend quatre espèces appartenant à trois genres, dont la plupart montrent une ressemblance avec les représentants du Triassique de la faune de l'Australie et une partie d'entre elles avec les formes du Permien supérieur de la Préouralie.

La revue sommaire de la composition des divers ordres d'insectes dont les restes ont été étudiés dans des dépôts paléozoïques du sud de la Sibérie, a démontré la grande originalité de tout ce complexe faunistique, qui se distingue beaucoup des autres faunes permiennes ou du Carbonifère supérieur du même âge. Ces traits caractéristiques des insectes paléozoïques du sud de la Sibérie, peuvent être définis comme suit:

1) Le petit nombre de restes de Palaeoptères dans les dépôts du Carbonifère supérieur et du Permien inférieur et leur absence dans le Permien supérieur.

2) L'abondance exceptionnelle de Coléoptères dans les faunes permiennes.

3). La grande variété de Mécoptères du sous-ordre des Protomecoptera.

4). La grande originalité de tous les groupes de la faune, exprimée par l'endémisme non seulement des genres (4/5 des genres étant endémiques), mais aussi des familles (presque la moitié des familles sont décrites comme étant nouvelles).

5) La présence de certains insectes permettant de faire des conclusions précieuses sur la phylogénie. Comme exemples: les Blattoprosbolidae qui se rapprochent des Homoptères et Blattodea; la découverte des Glosselytrodea, les plus primitifs; des familles Eglosselytridae et Permoberothidae nombreux Homoptères; l'importance de la plus ancienne trouvaille des Trichoptères; enfin, la diversité des Cupidae présentant, à ce que l'on croit, un des groupes ancestraux des familles des Coléoptères du Mésocénozoïque.

En considération des traits divers du complexe des insectes paléozoïques du sud de la Sibérie, il est possible de figurer les conditions climatiques particulières du sud de la Sibérie, à la période du Permien, dans le continent angarien. Le petit nombre de Palaeoptères et des Blattoïdes, la présence de Mécoptères primitivement poilus, l'abondance de Coleoptères et la multiplicité des espèces d'Homoptères, nous permettent de conclure que le climat du territoire du sud de la Sibérie, au temps du Permien, était tempéré. Les complexes permiens connus de l'Europe et des Amériques devaient posséder un climat tout autre, plus chaud et probablement subtropique. La faune permienne de l'Australie ressemble plus à celle du sud de la Sibérie, mais elle est encore trop insuffisamment étudiée pour nous permettre une comparaison adéquate.

Section

on

ARACHNIDA AND OTHER LAND ARTHROPODS

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Section Editor

H. H. J. Nesbitt

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The Evolution of Exoskeletons and Mite Phylogeny

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There seems to be widespread feeling that the family classification of mites is seriously confused. For example, the water-mites are broken up into forty or more families and the groupings above the family level are not especially helpful in making identifications and also fail to express phylogeny. These shortcomings seem to result from an inadequate understanding of the relationships and phylogeny above the family level. This paper will be concerned with phylogeny on higher levels, and I will attempt to explain some of the strong and weak points of our present system as a function of the methods and data that are used in mite systematics, and after that discussion related problems of a strictly taxonomic nature will be briefly mentioned.

Any attempt to evaluate current knowledge and seek new directions inevitably appears to aim criticism at previous workers for their lack of vision. In spite of appearances to that effect, the matters discussed below would not have been apparent without the carefully recorded data that has been arranged in an orderly fashion by such workers as Koenike, Piersig, Walter, Karl Viets, and Lundblad. New patterns emerge from their studies that seem to show approaches to higher classification, and my speculations along those lines rest on a great body of work of an exceptionally high level.

Our knowledge of mite relationships is based almost exclusively on comparisons of exoskeletal anatomy. This is not surprising for external anatomy forms the main basis for the classification of every major arthropod group, and when tested against information from other sources the data of external anatomy has proven generally valid. It seems to me that the widespread initial use of external anatomy was dictated by convenience at a time when the categorization of a multitude of undescribed forms was the major task confronting taxonomists. Fortunately these convenient characters have proven to be quite reliable in most arthropod groups and the reason for this is clear.

Most arthropods are large enough to require a nearly complete external skeleton for support of the body and appendages. Membranous areas are strictly functional; they either provide the flexibility that is essential for movable joints, or else allow for expansion of the abdomen for breathing or growth. Any fusion, appearance, loss, or alteration in the shape of a sclerite in such a fully armored form is likely to be easily recognized in the modified sclerite itself as well as in the neighboring sclerites. Of course, interpretation of these variations is not always easy, but, as a general rule, the phylogeny of the exoskeleton of larger arthropods can be traced as successive modifications of homologous sclerites. Thus, the inherent properties of the exoskeleton of large arthropods tend to make it an excellent indicator of phylogeny.

This is not the case in the Acarina. We are dealing with animals so small that extensive body sclerites are an encumbrance present only in specialized forms; thus the only sclerites that appear to be homologous throughout the order are the segments of the legs. Body sclerites are readily developed or lost and a sclerite may be modified in many ways without affecting other parts of the exoskeleton. Hence, our classification can consider only the evolution that followed the acquisition of body sclerites and the development of exoskeletons was a fairly recent event in the evolution of mites. The nearly exclusive use of the exoskeleton in mite classification appears to have directed attention to recent phyletic trends, leaving us with little or no knowledge of major lines of great age.

Some promising approaches to the understanding of major phyletic lines can be shown by way of an example taken from the water-mites, a group in which the morphology and biology are especially well-known. Generalized water-mites do not seem to need any body sclerites and the only sclerites that are homologous throughout the group are the segments of the appendages. Efficiency in either the crawling or swimming of aquatic mites requires sclerotization of the body in order to provide attachments for the especially strong muscles that are characteristic of highly adapted crawling or swimming forms. These body sclerites may come from four sources each of which has been used singly or in combination in many different lines.

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Sclerites of the leg bases (coxae) may expand to encase the body and there are two phyletic lines in which the coxae alone have almost completely encased the body. In the genus *Piersigia* the sclerites that form the major portion of the exoskeleton are the expanded sclerotized margins of glandular pores in the integument. More commonly the body sclerites result either from the sclerotization of large areas of the integument with no local precursors at all, or else from the sclerotization of muscle insertions on the body wall and expansion from these centers.

In specialized swimmers such as the Pionidae and Arrenuridae an exoskeleton may develop by expansion of the coxae, or by extensive sclerotization of membranous areas, but it commonly involves both sources. The extensive exoskeleton of specialized walking forms normally develops from sclerotization of the insertions of dorso-ventral muscles. The reasons for these rough correlations between locomotor habits and exoskeleton are partly clarified through a consideration of the functions of the sclerites. Walking forms evidently require a high degree of body turgor for extension of the legs. This turgor is developed by action of the dorso-ventral muscles, and as these muscles increase in size their attachments become sclerotized and expand to produce compound plates such as in Thyasidae and Sperchonidae. In swimming the muscles acting upon the basal leg segment tend to be longer and more powerful which results in an expansion of the coxae or coxal apodemes for the insertion of these modified muscles. Extension occurs just at the beginning of the power stroke when water resistance would naturally assist to straighten out the leg; hence, there is no great need for high body turgor. The remaining membranous areas of the body often become sclerotized in swimming forms but the reasons for this are not clear.

Sometimes sclerites are developed in order to alter body shape. The usual spherical shape of a soft-bodied form is a limitation in some habitats and about the only way of altering the body shape is through body plates. Secretive forms of swift streams are very thin and flattened, and the shape seems to result from extensive flat dorsal and ventral plates. These plates usually result from the thickening of extensive membranous areas and this is another modification that has occurred many times within the water-mites. Members of the families Axonopsidae and Torrenticolidae show such modifications.

I believe that primitive water-mites were unspecialized as to mode of locomotion and that they had no sclerites other than the segments of the appendages. Many such forms are now extant; the Protziidae and Limnocharidae are such forms. If the phylogeny of water-mites is traced from exoskeletal data, as present knowledge forces me to do, I must picture the ancestral form as a relatively uniform stock that persisted over some time and gave rise to some 15 or 20 stocks each of which evolved a peculiar exoskeleton. Each of these lines are now classified as a family or closely related group of families.

This phylogeny, based on exoskeleton, can be correct only if the ancestral stock did not evolve any special features other than exoskeletons during the time that it gave rise to the fifteen or more stocks we now recognize. There is no reason to believe that the ancestral stock was stable in every feature except the exoskeleton but this conclusion is inherent in modern taxonomic concepts. There is no data relative to this conclusion, so it stands as a glaring weakness in the present classification of water-mites, and since the exoskeleton is given similar emphasis in other groups I suspect that it may apply to many other groups of mites.

Carl Bader has recently published data that tests the phylogeny of exoskeletons against that of the mid-gut (Bader, 1954). The mid-guts of common European genera were compared and he concluded that there were four lines of evolution in the mid-gut as compared with fifteen or so in the exoskeleton. Data on the life history and larvae of water-mites seems to support Bader's conclusions. These studies of internal anatomy, the various life history stages, and behavioral traits together with an attempt to understand how the exoskeleton actually works and evolves show the way for a rigorous testing of present concepts of phylogeny.

From a strictly logical basis it seems that the exoskeleton of Acarina may not be as reliable a feature as it is in larger arthropods simply because the primitive mites were so small that they could have undergone considerable evolution while still soft bodied, and therefore the exoskeleton may give an erroneous picture of phylogeny. It is important that this argument should precede detailed consideration of the problem mentioned at first, that is, what to do about the congestion between families and the order, for it is obvious that my misgivings about present classification will make the discussion of this serious practical problem largely academic.

The existing confusion in family classification may not be due to the classification but to one's concepts of the meaning of the categories, and such confusion would presumably disappear with better understanding. If part, or all, of the confusion is due to the classification itself, then there are two possible things wrong. The Acarina may have been mistakenly placed on too low a level and deserve elevation to a class, or else there may be a great excess of families and the solution is one of consolidating families.

The argument for the elevation of the Acarina to a class can be supported by comparisons between classes of arthropods, and at this time there seems to be no support or strong interest in this approach.

The second possibility, that of consolidating families, can be proven only by studies within the Acarina. Comparisons of families need to be undertaken and the bulk of this paper was concerned with various features of modern classification that have a bearing on this problem. It was concluded that the exoskeleton may not be a reliable phylogenetic character, and tentative evidence from several sources indicates that there may be far too many families, at least in the water-mites. If this should prove true, and generally applicable to other groups as well, many families may be consolidated and this might contribute a great deal to our understanding of phylogeny, as well as solving many of the taxonomic problems that now face us.

REFERENCE

Bader, C. 1954. Das Darmsystem der Hydracarinen. *Rev. Suisse d. Zool.* 61: 505–549.

A Preliminary Account of the Phylogeny of the Oribatei (Acarina: Sarcoptiformes)

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ABSTRACT

The problem of phylogeny in the oribatid mites is reviewed and discussed. The writer employs two existing cohorts, Aptyctima (Gr., unfolded) and Ptyctima (Gr., folded) as the subordinate categories in his placement of 34 families of these mites. Ten superfamilies are delineated on the basis of body form, genital plates, pteromorphae and other morphological features to accommodate the various families. The Aptyctima includes 9 superfamilies: Palaeacaroidea, Lohmannoidea, Nanhermannoidea, Hermannoidea, Carabodoidea, Eremaeidoidea, Oribatelloidea, Oribatuloidea and Pelopoidea. The first six of these superfamilies are comprised of families in the subcohort Apterogasterina of European classification. The last three superfamilies include the families of mites in the subcohort Pterogasterina in older taxonomic literature. Neither of these subcohorts is used by the writer, however. The single superfamily in the cohort Ptyctima is Phthiracaroidea, comprising three families. An attempt is made to include families of rather close morphological similarity in a superfamily. The superfamilies in turn are arranged in series within each cohort to demonstrate these assumed affinities. The Palaeacaroidea are postulated to possess the closest affinities to the Acaridiae of the suborder Sarcoptiformes.

Two principal taxonomic cohorts exist in the suborder Sarcoptiformes, the Acaridiae and the Oribatei. Yunker (1955) described the higher categories of the Acaridiae and suggested probable phylogenetic relationships within that cohort. The following preliminary account constitutes a similar delineation of the groups within the cohort Oribatei.

The British acarologist Michael (1898) used the family name *Oribatidae* and not the term of the supercohort *Oribatei* Dugès, 1834, for the seven subfamilies of mites which he classified. Banks (1915) erected the superfamily *Oribatoidea* with two families, *Oribatidae* and *Hoplodermatidae*. Previously, Ewing (1913) had proposed the suborder *Heterotracheata* in which he placed the beetle mites, the tarsonemids and the pediculoidids. In this arrangement the beetle mites comprised two of three sections, Section *Ginglymosoma* with the family *Hoplodermidae* and Section *Scleroderma* which included the families *Hypochthoniidae*, *Nothridae* and *Oribatidae*. In a later publication Ewing (1917) arranged fourteen subfamilies of these mites within these four families.

Jacot (1925) used the name *Oribatoidea* for this group and postulated the taxonomic and phylogenetic relationships within the category and with other acarines. He specifically dealt with similarities within the superfamily and included some ecological data. He changed the subphalanges *Apterogasterina* and *Pterogasterina* of Michael to family status and included most of the oribatids in eleven subfamilies. The same author (1929) placed all of the beetle mites in two families, the *Oribatidae* and the *Phthiracaridae* within the superfamily *Oribatoidea*.

Concurrently the works of Sellnick (1929), Vitzthum (1929) and Willmann (1931) changed the taxonomy of the oribatids and extended the use of subordinal designations. More recently Grandjean (1953) established a classification based primarily upon development. His presentation involved a complicated taxonomic revision concerned with morphological features of larval and nymphal stages. He attempted to resolve the classification of the Oribatei into one system so that this group, with varying developmental stages, would not have two separate classification systems for nymphs and adults, respectively, as is the case in several acarine groups. He cited eleven natural groups of unequal dimensions and status, but all of the same rank. Some of the families in his admittedly provisional classification were grouped in superfamilies. Other families were retained at the superfamily level. The category *Circumdehiscentiae* Grandjean employed to include a great many families, the relationships of which cannot be completely understood at the present time.

This paper suggests a schematic representation (Figs. 1 and 2) of the taxonomic and phylogenetic relationships of adult Oribatei based upon fairly obvious morphological features. In some respects this arrangement may appear quite simple, and there is a danger of over-simplification in taxonomy. On the other hand, there may be a problem in a system

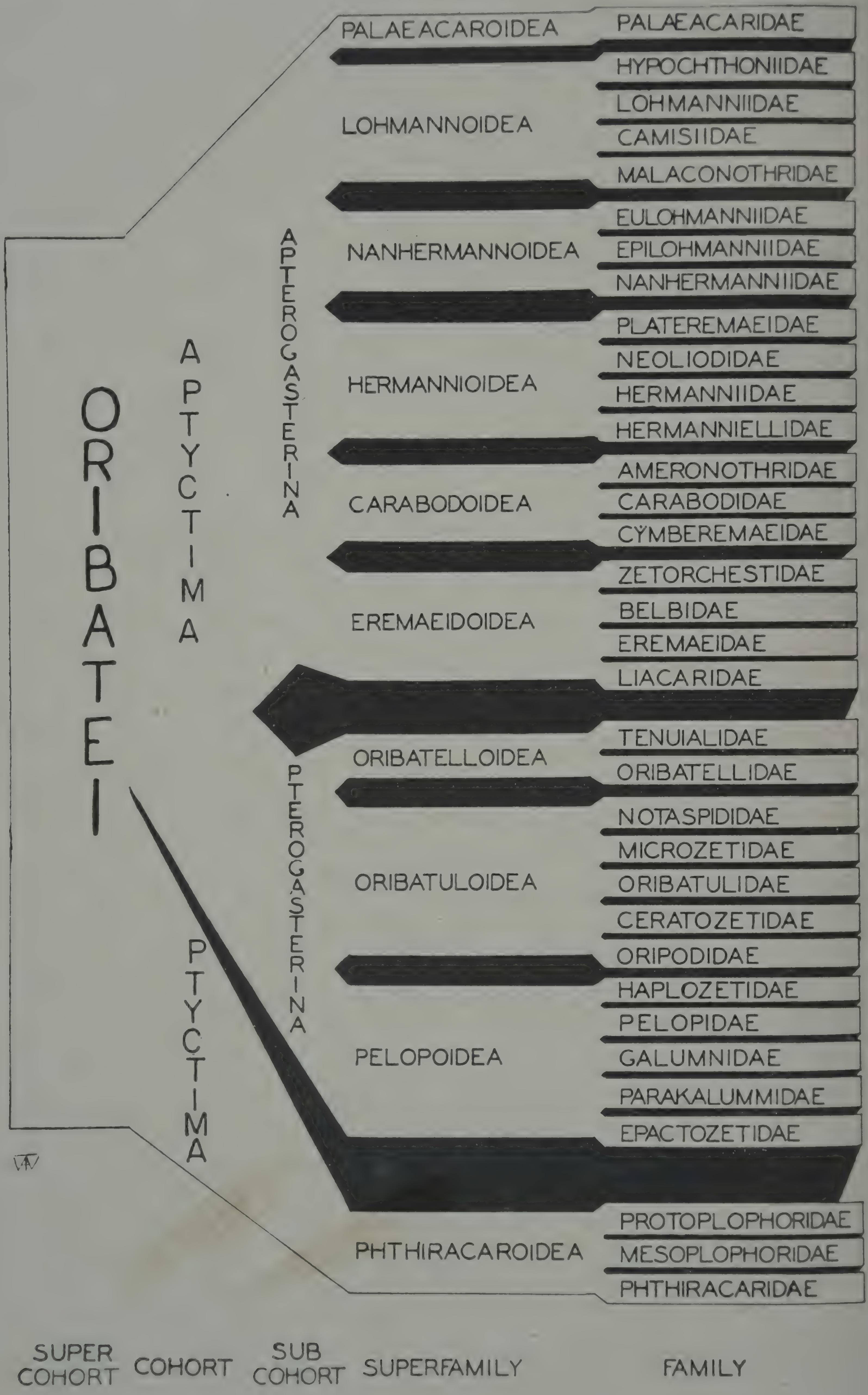
PALAEACAROIDEA
PALAEACARIDAE
HYPOCHTHONIIDAE
LOHMANNOIDEA
LOHMANNIIDAE
CAMISIIDAE
MALACONOTHRIDAE
EULOHMANNIIDAE
NANHERMANNOIDEA
EPILOHMANNIIDAE
NANHERMANNIIDAE
PLATEREMAEIDAE
HERMANNIOIDEA
NEOLIODIDAE
HERMANNIIDAE
HERMANNIELLIDAE
AMERONOTHRIDAE
CARABODOIDEA
CARABODIDAE
CYMBEREMAEIDAE
ZETORCHESTIDAE
EREMAEIDOIDEA
BELBIDAE
EREMAEIDAE
LIACARIDAE
TENUIALIDAE
ORIBATELLOIDEA
ORIBATELLIDAE
NOTASPIDIDAE
MICROZETIDAE
ORIBATULOIDEA
ORIBATULIDAE
CERATOZETIDAE
ORIPODIDAE
HAPLOZETIDAE
PELOPIDAE
PELOPOIDEA
GALUMNIDAE
PARAKALUMMIDAE
EPACTOZETIDAE
PROTOPLOPHORIDAE
PHTHIRACAROIDEA
MESOPLOPHORIDAE
PHTHIRACARIDAE
ORIBATEI
APTYCTIMA
PTYCTIMA
APTEROGASTERINA
PTEROGASTERINA
SUPER COHORT
COHORT
SUB COHORT
SUPERFAMILY
FAMILY

Fig. 1.

that is so complex that its utility is curtailed because of excessive details. It is hoped that the following arrangement is within the middle ground between these two extremes.

In some instances the current proposal is different from other arrangements in the literature. Such differences of opinion are frequent in taxonomic studies. They are due,

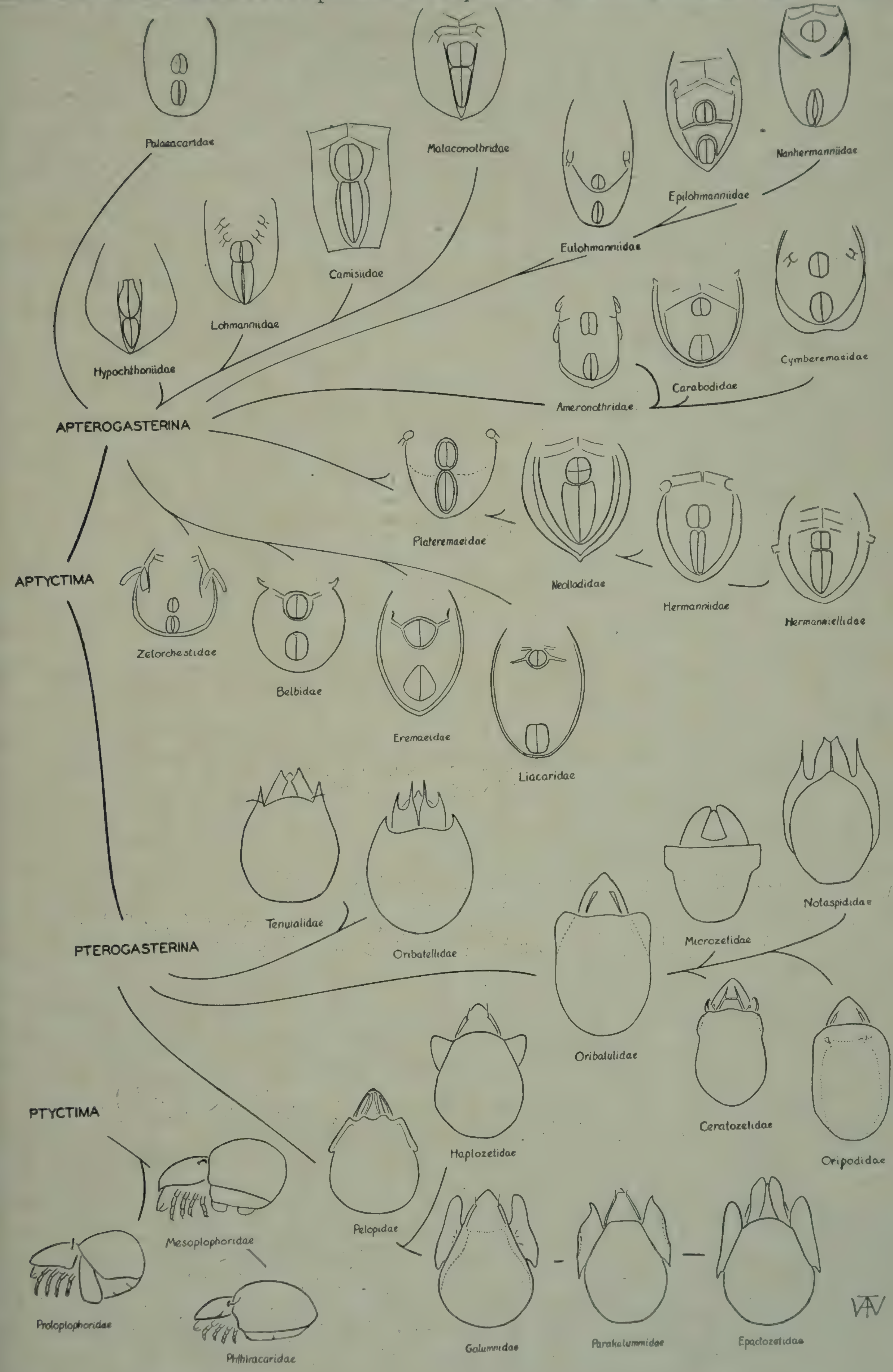
Palaeacaridae
Malaconothridae
Nanhermanniidae
Epilohmanniidae
Camisiidae
Eulohmanniidae
Lohmanniidae
Hypochthoniidae
Carabodidae
Cymberemaeidae
Ameronothridae
APTEROGASTERINA
Plateremaeidae
Neoliodidae
Hermanniidae
Hermanniellidae
APTYCTIMA
Zetorchestidae
Belbidae
Eremaeidae
Liacaridae
Tenuialidae
Oribatellidae
Notaspididae
Microzetidae
PTEROGASTERINA
Oribatulidae
Haplozetidae
Ceratozetidae
Oripodidae
PTYCTIMA
Mesoplophoridae
Pelopidae
Protoplophoridae
Phthiracaridae
Galumnidae
Parakalummidae
Epactozetidae
VAV

Fig. 2.

in this case, in part, to the writer's aversion to excessive splitting and to an admission of an apparent necessity for the use of a category larger than family to handle the diverse groups of the Oribatei. The oribatids seem to fall into natural groupings based on adult characters and into which they may be placed for general identification. It is hoped that this proposal will facilitate this placement. In the opinion of the writer the use of superfamilies in such an arrangement is justified because of the facility of grouping which results and the apparent phylogeny which may be demonstrated.

There are some aspects of this presentation which are only partially admissible in the face of known evidence. One is constantly aware of probable phylogenetic relationships among animals, however, and at least suspects the possible avenues of development.

The inferences and postulations in this paper are derived from a study of the most probable and logical arrangement of known oribatids. The characters employed as bases for this scheme include body form, lamellae, arrangement of genital and anal plates, presence, absence, shape and mobility of pteromorphae. The arrangements follow partially the categorical designations of European workers. The supercohort *Oribatei* and two cohorts, *Aptyctima* and *Ptyctima* are employed. The existing subphalanges *Apterogasterina* and *Pterogasterina* are used as subcohorts of the *Aptyctima*, although there is no corresponding designation in the *Ptyctima*.

Suggested Classification and Diagnosis

- Suborder Sarcoptiformes
  - Supercohort Oribatei
    - Cohort Aptyctima
      - Subcohort Apterogasterina
        - Superfamily Palaeacaroidea
          - Family Palaeacaridae
        - Superfamily Lohmannoidea
          - Family Hypochthoniidae
          - Family Lohmanniidae
          - Family Camisiidae
          - Family Malaconothridae
        - Superfamily Nanhermannoidea
          - Family Eulohmanniidae
          - Family Epilohmanniidae
          - Family Nanhermanniidae
        - Superfamily Hermannioidea
          - Family Plateremaeidae
          - Family Neoliodidae
          - Family Hermanniidae
          - Family Hermanniellidae
        - Superfamily Carabodoidea
          - Family Ameronothridae
          - Family Carabodidae
          - Family Cymberemaeidae
        - Superfamily Eremaeidoidea
          - ?Family Zetorchestidae
          - (?Family Gustaviidae)
          - Family Belbidae
          - Family Eremaeidae
          - Family Liacaridae
      - Subcohort Pterogasterina
        - Superfamily Oribatelloidea
          - Family Tenuialidae
          - Family Oribatellidae
        - Superfamily Oribatuloidea
          - Family Notaspididae
          - Family Microzetidae
          - Family Oribatulidae
          - Family Ceratozetidae
          - Family Oripodidae
        - Superfamily Pelopoidea
          - Family Haplozetidae
          - Family Pelopidae
          - Family Galumnidae
          - Family Parakalummidae
          - Family Epactozetidae
    - Cohort Ptyctima
      - Superfamily Phthiracaroidea
        - Family Protoplophoridae
        - Family Mesoplophoridae
        - Family Phthiracaridae

The Cohort Oribatei is characterized by integument that is usually strongly sclerotized, frequently dark colored and by the presence of pseudostigmata and pseudostigmatic organs. The detailed variations in these major features are quite numerous and will not be elucidated here. This paper concerns the general characteristics which help to separate the larger groups in the cohort.

There are six superfamilies in the subcohort Apterogasterina. Of these proposed superfamilies the most primitive is the Palaeacaroidea. Mites of this group are weakly sclerotized, the chelicerae are large and uncovered, and there are five pairs of propodosomal setae. The pseudostigmata and pseudostigmatic organs are quite simple. The general body shape and genital openings of *Acaronychus tragardhi* Grandjean resemble *Acarus siro* L., a member of the Acaridiae. These features are suggestive of a phylogenetic relationship.

This opinion was believed corroborated in initial observations in which the writer saw what appeared to be genital suckers in the former species. Subsequent study, however, showed these to be distal tips of oviposition organs seen through the integument. Nevertheless, the writer is of the opinion that the Palaeacaroidea constitute the representatives of the Oribatei with the closest affinities to the Acaridiae, because they so closely resemble the latter.

The remaining superfamilies of the Aptyctima include mites in which sclerotization is relatively prominent. Some species are less sclerotized than others, but none is so weakly sclerotized as the Palaeacaroids.

Probably the most conspicuous characteristics of the Lohmannoidea are the elongated bodies and the long triangle formed by the contiguous genital and anal plates. In some instances the elongate body is oval or rotund as in the Malaconothridae and Hypochthoniidae, or angular as in the Camisiidae. The Lohmanniidae includes species which are somewhat depressed. All of these families, however, exhibit the triangular, contiguous genital and anal plates. The individual variations in setation and integumental reticulations are many and in these families one observes some of the simpler oribatids.

The Nanhermannoidea comprises mites in which there is a suture between the genital and anal openings. In Nanhermanniidae this suture is crescentic and does not completely separate the two openings. The suture of the Eulohmanniidae is slight and appears to be a shallow depression in most of the specimens observed by the writer. The suture of the Epilohmanniidae forms the juncture between two sets of ventral plates which surround the genital and anal openings.

Mites of the superfamily Hermannioidea are nearly always globular in appearance and possess contiguous genital and anal plates. The Plateremaeidae, Hermanniellidae and Neoliodidae frequently carry cast skins on the dorsum of the hysterosoma. In the latter family the genital plates are bisected by a transverse suture suggestive of specialization. In a similar way Hermanniellids exhibit a short pedunculate, glandular opening on each side of the hysterosoma. In Hermanniidae the anal plates are narrow and about a third longer than the genital plates.

A depressed, disc-like body is one of the features which distinguishes most mites of the Carabodidae. Both Carabodidae and Cymberemaeidae include emarginate species with depressed hysterosomas. The Ameronothridae appear the least flattened. In all of these families the integument is usually highly reticulate or filigreed. Frequently a cerotegument is present over the body and all of the mites in this superfamily show the genital and anal openings separated by the ventral plate.

The Eremaeidoidea comprises families in which the apodemata IV usually surround the genital opening and in which the legs are frequently composed of modified or expanded segments. Placement of the Zetorchestidae in this superfamily is partly a matter of convenience and the writer defers the exact position of the latter family and the family Gustaviidae, although both most probably belong in this group. The family Eremaeidae appears to constitute development intermediate between the species of the Belbidae and Liacaridae. Both of the latter families exhibit the feature of the fourth apodeme, but variations exist in the approximations and shapes of the genital and anal openings. The legs of the Belbidae may be extremely long and these mites may carry secretions or cast skins on their dorsal surfaces. The hysterosoma of a belbid is usually globular, in contrast to the oval or slightly arched bodies of the other two families.

The Liacaridae is probably the family with the closest affinity to the remaining three superfamilies, particularly to the family Tenuialidae in the superfamily Oribatelloidea (Woolley and Higgins, 1955).

The Oribatelloidea is the first of three superfamilies within the Aptyctima in which the mites exhibit pteromorphae, which connote the term Pterogasterina. There are two families in this superfamily both of which exhibit immovable pteromorphae that project anteriorly beyond the margin of the hysterosoma. The Tenuialidae constitutes a group of mites in which the pteromorphae are fixed, triangular projections, extended forward but not curved ventrad. The lamellae of these mites are flattened plates which may extend only slightly beyond the rostrum. The pteromorphae of the Oribatellidae do not curve ventrally nor do their anterior tips project beyond the opisthosoma. The lamellae are well developed, flattened plates which nearly cover the propodosoma and have deeply cleft anterior margins.

The mites of the next superfamily have laterally-projected pteromorphae. The five families in the Oribatuloidea represent, in the writer's opinion, groups of mites which have developed in two divergent directions from a single point. This point is considered to be close to the morphological pattern exhibited by the family Oribatulidae. In this family the pteromorphae are not emarginate and do not curve ventrad over the legs, but curve backward from the dorsal aspect to form a translucent shoulder patch at the antero-lateral margins of the hysterosoma. This shoulder may be rather large and obvious (*Protoschelobates*) or quite small (*Eporibatula*).

From the assumed middle ground of the oribatulids the families Microzetidae and Notaspididae appear to have developed in one direction, Ceratozetidae and Oripodidae in another. The pteromorphae of the Microzetidae are expanded slightly, forming squarish shoulders which have accompanied an extensive development of the lamellae. The Notaspididae exhibit pteromorphae each of which is produced anteriorly into a long spine. These mites, too, have developed broad lamellae that appear fused to each other along their medial margins.

The Ceratozetidae and the Oripodidae exhibit a reduction in the size of the lamellae and a more extensive development of the pteromorphae than the Oribatulidae, but not as great as the Notaspididae or Microzetidae. The pteromorphae of the ceratozetids do not project anteriorly, but they may extend ventrad slightly and may be expanded posteriorly. The lamellae of the Ceratozetidae typically are fused along their medial margins and project freely at their distal tips. In the Oropodidae the pteromorphae have coalesced and expanded to form a type of carapace that covers the pseudostigmata and parts of the lamellae and propodosoma. The lamellae are narrow bars fused to the propodosoma and exposed for part of their lengths anterior to the coalesced pteromorphal cover.

The superfamily Pelopoidea includes the remaining families of aptyctimous mites. All of these families exhibit pteromorphae which are hinged and movable. The family Pelopidae appears to constitute the intermediate type with broad, ventrally curved pteromorphae, which may extend anteriorly, but not in a posterior point. The family Haplozetidae exhibits relatively smaller, more pointed pteromorphae that extend antero-laterad. The lamellae of these two families differ markedly. Pelopids show rather broad lamellae. Haplozetids have developed narrow lamellae near the lateral margins of the propodosoma, which condition resembles the lamellae of the Galumnidae, another family in this major group.

Mites of the family Galumnidae possess large, expanded pteromorphae which may be depressed to enclose the legs beneath them. In such a position the body outline becomes drop-shaped, the propodosoma making the narrower end. The pteromorphae are rounded anteriorly and posteriorly. Their ends extend beyond the limits of the hinged margins. The Parakalummidae are very similar to the Galumnidae, but their pteromorphae have developed pointed ends and the propodosoma and hysterosoma are separated by a suture, which may or may not be present in the Galumnidae. Both of these families exhibit weakly developed lamellae or the lamellae may be lacking.

The last of the pterogasterine families is Epactozetidae. The ends of the pteromorphae of these mites project in both directions beyond the hinge margin. The mites are distinguished from others in this superfamily by the extremely large lamellae, which may cover most of the propodosoma.

Although the Galumnidae, Parakalummidae and Epactozetidae are currently separate in oribatid taxonomy, the writer suggests that possibly these families constitute subfamilial groups within a single family. Conclusive evidence in support of this supposition is not available at the present time. Specific studies of these groups may indicate, however, that the characteristics of genital setae, propodosomal suture, and variations of lamellae and pteromorphae are insufficient to vindicate separate familial designations for each of these groups.

The Ptyctima is the other principal cohort in the Oribatei and comprises those mites in which an aspis is present and beneath which the legs may be retracted when the aspis is closed tightly against the notogaster. This hinged action is indicative of the cohort name, which means "folded."

The three families included in the superfamily Phthiracaroidea are so different from the rest of the Oribatei that it is obvious why they are separated taxonomically. Yet, it is possible that the phylogeny of these families has been misinterpreted. They may have closer affinities with camisiid apterogasterines than is currently indicated. If corroborative evidence for such an assumption is forthcoming, it will probably result from investigations of comparative development.

There appears to be a gradual transition within the superfamily Phthiracaroidea. The Mesoplophoridae are probably intermediate with fewer plates and less sclerotization. Protoplophoridae and Phthiracaridae seem to be bilaterally placed and exhibit differential amounts of sclerotization and compression.

SUMMARY

Investigations of the taxonomy of oribatid mites lead the writer to conclude that the supercohort Oribatei may logically be subdivided into 9 superfamilies in the cohort Aptyctima and one superfamily in the cohort Ptyctima. The Palaeacaroidea, Lohmannoidea, Nanhermannoidea, Hermannioidea, Carabodoidea and Eremaeidoidea comprise the superfamilies in the subcohort Apterogasterina. The Oribatelloidea, Oribatuloidea and Pelopoidea constitute the superfamilies of the subcohort Pterogasterina. The three families of ptyctimous mites are included in the superfamily Phthiracaroidea. All of the families and their proposed relationships and affinities are described on the basis of morphology and indicated in modified dendrograms (Plates I & II) to show the phylogeny.

REFERENCES

Banks, N. 1915. The acarina or mites. *USDA Report* 108. U.S. Government Printing Office.

Ewing, H. E. 1913. New Acarina. *Bull. Amer. Mus. Nat. Hist.* 32: 93–121.

Ewing, H. E. 1917. A synopsis of the genera of beetle mites with special reference to the North American fauna. *Ann. Ent. Soc. Amer.* 10: 117–132.

Grandjean, F. 1953. Essai de classification des Oribates. *Bull. Soc. Zool. France* 78: 421–446.

Jacot, A. P. 1925. Phylogeny in the Oribatoidea. *Amer. Nat.* 59: 272–279.

Jacot, A. P. 1929. Genera of pterogasterine Oribatidae. *Trans. Amer. Mic. Soc.* 48: 416–430.

Michael, A. D. 1898. Oribatidae. *In* Das Tierreich 3: 1–93.

Sellnick, M. 1929. Formenkreis: Hornmilben, Oribatei. *In* Die Tierwelt Mitteleuropas 3: 1–42.

Vitzthum, H. 1929. Milben. Acari. *In* Die Tierwelt Mitteleuropas 3: 1–112.

Willmann, K. 1931. Moosmilben oder Oribatiden (Oribatei). *In* Tierwelt Deutschlands 22: 79–200.

Woolley, T. A., and H. G. Higgins. 1955. A review of the family Tenuialidae with a description of a new species from Colorado and Utah. *Bull. Chicago Acad. Sci.* 10: 45–60.

Yunker, C. E. 1955. A proposed classification of the Acaridiae. *Proc. Helm. Soc. Wash.* 22: 98–105.

Leg Segmentation in the Acarina and other Arachnida

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ABSTRACT

Correlated with general size reduction, many of the organs and organ systems in the Acarina have become reduced and simplified. In some cases these reductions and losses of structures have tended to obscure phylogenetic relationships, while in others the relationships are clarified by the simplifications. The musculature and segmentation of the legs of the mites are examples of the latter. In the Acarina, the extensors of the more distal segments of the legs and the ventral branches of the flexors have been lost, leaving these muscles as simple, unbranched bands.

In the mites of the genus Opilioacarus, *the most primitive living members of the order, a muscle arising in the "basitarsus" and inserting on the "telotarsus" indicates that these segments are actually the tibia and tarsus. With this interpretation, the pretarsal muscles originate in the tibia and the acarines are brought into line with the other arachnids. However, this leaves two segments between the tibia and femur. The two segments appear to be homologous with the single patellar segment of other Arachnida. The opilioacarids also possess two trochanters on some legs, as do other arachnids. Comparative studies or higher acarines indicate that the second trochanter or prefemur has fused with the femur and the tibia and tarsus have fused in most cases. Two genual or patellar segments are present in all of the mites examined. In the Acarina there appear to be nine primary leg segments with muscles inserting on their bases.*

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Observations on the Mating Habits of Two Scorpions, *Leiurus quinquestriatus* H. et E. and *Buthotus judaicus* E.S.

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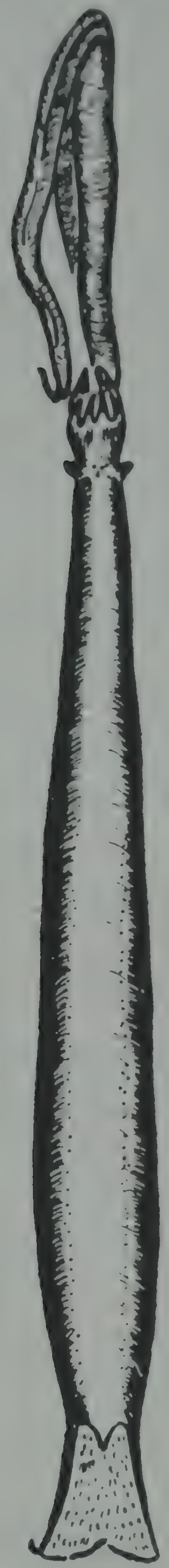
In a recent study Vachon (1952) stated that little is known about the mating of Scorpions. Fabre (1907) described a "promenade à deux" when two Scorpions are moving together holding each other by the pedipalps. According to him (loc. cit.) the male starts disclosing his intentions by presenting "l'arbre droit" i.e. raising his postabdomen and crossing it with that of the female. Pavlovsky (1924) in a study of the female genitalia of the Scorpions coined the name of *spermatocleithrum* for the chitinous mass which he found in the vaginal opening of the fecondated female. He suggested that this structure is part of *spermatophore* excreted by the paraxial organ of the male. According to Pavlovsky (loc. cit.) this spermatocleithrum consists of the central chitinous part found in the vaginal opening and two whitish diverticula situated at the ends of the oviducts. These diverticula may be formed by one of the seminal sacks constituting part of the paraxial organ. This author pointed out in the same paper that the introduction of the spermatophore may be similar to that found in *Solifuga* by Birula (1894) and in *Pseudoscorpions* by Kew (1912). Vachon (1952) has found several times in dissected Scorpions that the proximal ends of the paraxial organs meet together and he suggested that the expulsion of the paraxial organs may result in the formation of a true penis which is later separated from the body of the male after copulation.

On the 24 of April, 1956 and again on the second of June of the same year we were able to observe the beginning of the mating by *Leiurus quinquestriatus* H. et E. and *Buthotus judaicus* E.S. respectively (Shulov, in press). Although in both cases no introduction of spermia into female genitalia actually took place, it seems, that our observations add some new facts to the understanding of these obscure habits.

Leiurus quinquestriatus H. et E.

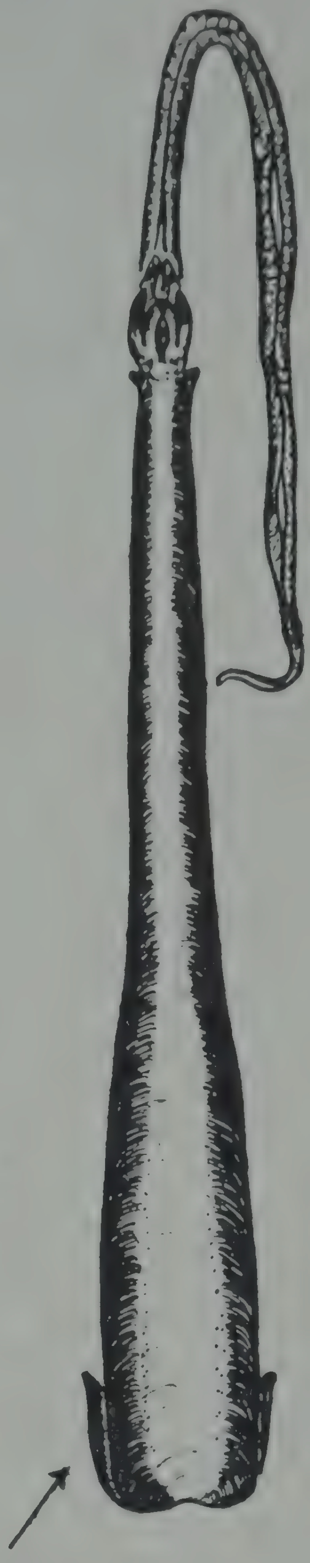
At 12.30, 24.4. 1956, an adult male was introduced into a jar containing a female. Both scorpions had been collected a few days previously in the environs of Jerusalem. The male jumped immediately towards the female and seized her pedipalps with his. The reaction of the female was rather passive. The male started pulling the female towards him, paused and then pushed her back, repeating this procedure again and again. This action resulted in close touching of the *chelicerae* of both partners and of the front margins of their *carapaxes*. The body of the male trembled, the trembling being passed to the female through the pedipalps. During these movements the first pair of legs of the male drummed upon his own chelicerae and on the chelicerae, the legs and the *carapax* of the female, but did not reach the *pectines*. This drumming resembled similar movements of the male pedipalps of the Theridiid Spiders during the prenuptial courting. The pectines of the male were also active, their dents moving independently.

This courting continued for some 15 minutes. Then both partners paused facing each other. The male raised his prosoma to some 45°, his tail pressing against the soil. Suddenly he raised his prosoma higher and from the genital pore appeared a minute dark stick-like object. The ejection of this object continued for some 6–8 seconds, during which it was directed almost horizontally towards the female. When completely expulsed, this object fell to the ground, the scorpions separated and started running in the jar. The object was removed and found to be a spermatophore. The origin of the spermatophore from the double paraxial organ may be seen at the first glance. It appears that the dorso-medial *facies* of these organs meet together and form a complete chitinous tube bearing four pairs of lobes on its distal end where two fused *flagella* form an unpaired prolongation. The proximal end of the tube is continued in an "anchor piece". Thus the spermatophore consists of three parts: the anchor piece, the basal tube and the double flagellum (Fig. 1). The anchor piece about 1mm long has two chitinous processes between which a tough whitish membrane is spread. This structure forms an angle of some 80° with the basal tube. This latter, which corresponds to the double "charpente" of the paraxial organs of Vachon (1952) represents a hollow tube 7mm long and about 1mm broad in its proximal inflated

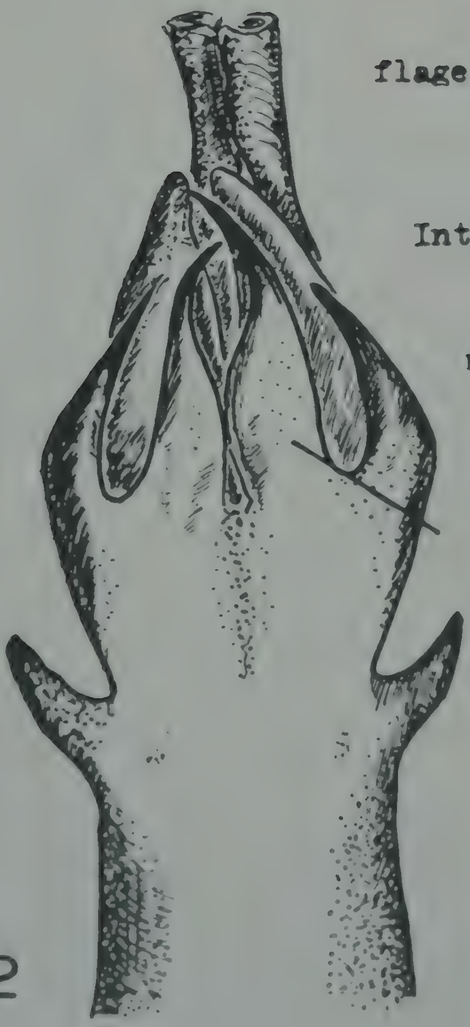


1

flagellum
basal tube
anchor - piece

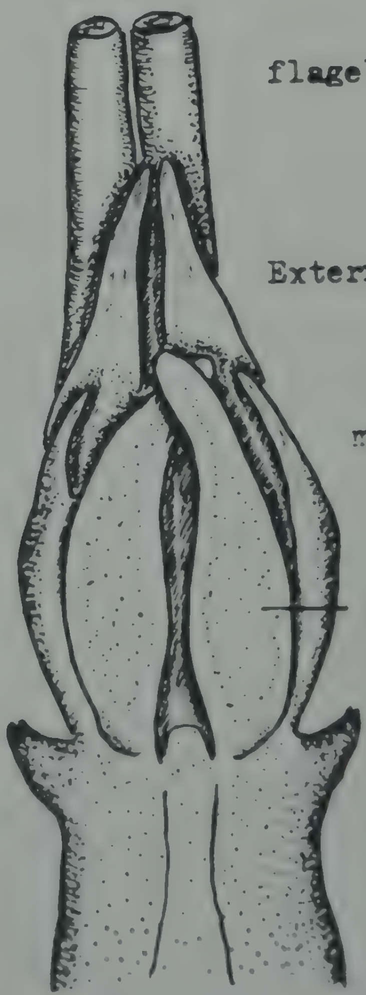


3



flagellum
Internal lobe
medial lobe
External lobe
basal lobe

2



flagellum
External lobe
medial lobe
Internal lobe
basal lobe

4

part. Seen dorsally it narrows gradually toward the distal end, when seen laterally however, the inflated part narrows abruptly leaving two thirds of the remaining length considerably thinner.

The denominations used by Vachon (1952) for the chitinous lobes of the paraxial organs fit equally well for the lobes of the basal tube of the spermatophore. The basal lobes are situated on the opposite lateral sides of the spermatophore serving perhaps for the anchoring in the walls of the vaginal opening. The remaining three pairs of *lobi* form the walls of the seminal passage on the distal end of the tube. The external lobes meet on the dorsal side, the internal lobes touch each other on the ventral side and the median ones form the lateral walls of the seminal passage (Fig. 2). The tube contains a whitish substance, apparently spermia. The flagellum is doubled almost along its whole length, the fissure, however, is not complete at the origin and at the end. The flagellum keeps the form of the *pars recta* and *pars reflexa* as it appears in the paraxial organ.

After this observation the jars where the scorpions were kept were thoroughly investigated and in one of them a spermatophore broken in three pieces was found. The anchor-piece was gummed to the paper on the bottom of the jar by a whitish substance, the basal tube and the flagellum were lying apart.

Four days after observation the male in question was dissected and both sheaths of the paraxial organs found empty. On the same day five adult males were dissected and their paraxial organs were found to be well developed and the seminal sacs full of sperms. In two of them two of the basal processes of the "charpente" from both sides were touching each other at their proximal ends. In two cases when they were put into a saline solution, the *flagella* began vermiform movements which continued for several hours. The adding of a few drops of the fluid squeezed from the genitalia of a fecondated female did not accelerate these movements.

Five adult females of *Leiurus quinquestriatus* taken from the field were dissected and their *Spermatocleithrum* removed. The basal part of it was found to consist of a shrunken, chitinous tube with tiny dark pieces which may be the remnants of the lobes of the spermatophore. The diverticula emerging at right angles from the distal end of the basal part consist of a tough whitish yellow substance; their form seems to confirm Pavlovsky's (1924) suggestion that there are residual parts of the seminal sacs of the paraxial organs.

Buthotus judaicus E.S.

At 10.30 on 2.5.1956, a male SA 1191 and a female Sco 450 were put together. Both had been isolated in the laboratory for some six months. The male started running about, resting at intervals. By 12.15 his movements had become accelerated and he caught the female's pedipalps with his. The male pulled the female toward himself, then relaxed the hold and pushed her back, repeated the performance several times, than paused and started again. Now and then one of the pedipalps of the female was freed and, shortly afterwards seized again. Then the male without loosening his grip of the female, raised high his prosoma and pressed it several times to the ground. The opercula of his genital opening were conspicuously thrown open. His legs trembled and this trembling was passed to the female by ways of the pedipalps. His forelegs drummed upon the legs and the fore margin of the carapax of the female. Suddenly he raised his prosoma and the pedipalps and the prosoma of the female and simultaneously the spermatophore appeared in the form of a tiny stick directed almost horizontally towards the female. The extrusion of the spermatophore continued for some 5 seconds. When fully protruded, the spermatophore bent down so that its anchor-piece reached the ground and became anchored in it. The flagellum remained attached to the genital opening of the male by its distal end and the male apparently was able to direct the spermatophore into the almost erect posture by pulling the flagellum. At the same time the male raised the prosoma of the female and pulled her violently towards himself. Immediately after, the female freed herself and started running about.

Fig. 1. Spermatophore of *Leiurus quinquestriatus*.

Fig. 2. Proximal end of same.

Fig. 3. Spermatophore of *Buthotus judaicus*.

Fig. 4. Proximal end of same. (The labels for the external and internal lobes were inadvertently reversed.

After few minutes when it was clear that the female failed to pay any attention to the spermatophore, it was removed from the jar. The anchor-piece was found to be gummed to the bottom by a tough whitish mass.

The spermatophore of *Buthotus judaicus* (Fig. 3) is similar in its size and shape to that of *Leiurus quinquestriatus*. The main differences are: The basal tube of the forms is clearly inflated in its proximal third when seen from the dorsal side, the gradual narrowing of the tube being visible only from the lateral side. The basal lobes of *Buthotus judaicus* are considerably shorter when seen from the dorsal side, their apex divided into two. The external lobi are longer and not pointed at their ends, the internal lobes being more attenuated towards their ends (Fig. 4).

Although no complete mating has so far been seen, the nuptial habits observed seem to warrant the following conclusions:

It appears that the mating process of these scorpions is similar to that described by Kew (1912) for the Pseudoscorpions where the male places his spermatophore on the ground and pulls the female against it. The spermatophore is formed from the paraxial organ just before the mating during 6–8 seconds. It is placed on the ground and sticks to it while the male is controlling the posture of the spermatophore and pulls the female towards it. The female receives the spermatophore into the vagina directly from the ground and a part of the spermatophore remains in her geninal opening. The spermatozoa are apparently pushed out of the spermatophore together with the remnants of the seminal sacs contained in it. The residual part of the spermatophore remains in the vagina and oviducts of the female in form of spermatocleithrum.

The *pectines* apparently play no direct part in the sexual intercourse. The movements of the dents seen may be described as an intensified action of the tactile organ serving a more general purpose.

The *promenade à deux* has been proved to be part of the mating habits but the *arbre droit* is not. The latter posture is observed frequently during the whole year when scorpions of the same as well as of opposite sex meet.

REFERENCES

Birula, A. 1894. Untersuchungen ueber den Bau der Geschlechtorgane bei den Galeodiden. *Horae Soc. Entomol. Rossicae* 28.

Fabre, J. H. 1907. Souvenirs entomologiques. 9e serie ed. *Delagrave*, Paris.

Kew, H. W. 1912. On the pairing of pseudoscorpions. *Zool. Soc. London* 376.

Pavlovsky, E. N. 1924. Skorpiotomische Mitteilungen IV. *Zool. Jahrb.* 46 *Abt. f. Anat.* 493.

Vachon, M. 1952. Etudes sur les scorpions. *Inst. Pasteur d'Algerie*, Alger.

Shulov, A., and P. Amitai. A contribution to the knowledge of the mating habits of the scorpions. *Bull. Res. Council of Israel*. (In press).

Records of Formosan Myriapods[1]

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CLASS DIPLOPODA

Order Polydesmida

1. *Epanerchodus orientalis orientalis* Attems, 1901. One female collected by Tsai Chu-Fa at Sze Tou Mountain, Hsin-Cho, May 6, 1956.

2. *Orthomorpha coarctata* (Saussure), 1860. 154 males and females collected by Tsai-Chu-Fa and Ho Ming-Chuan throughout Hua-Lien in January and February, 1955; one female taken by Miss Chu Pao-Ching at Taipei, on March 28, 1956; and one male and two females taken at University Farm on April 4, 1955, by Tsai Chia-Tai.

3. *Chamberlinius hualiensis* Wang, 1956. Two males and five females collected by Tsai Chu-Fa at Taruko, Hualien, February, 1955; three males and two femalse taken by the same collector at Milan, Hualien, January, 1955; one male and seven females taken by Tsai Chu-Fa and Ho Ming-Chuan at Tso-Kiang, Hualien, January, 1955; and one male and three females collected by Tsai Chu-Fa at Kaliwan, Hualien, 1955.

4. *Rhysolus uraensis* Wang, 1956. One male collected by Prof. Yu Chin-San at Urai, Taipei, February 2, 1955.

CLASS CHILOPODA

Order Geophilida

5. *Orphnaeus brevilabiatus* (Newport), 1845. One specimen taken on the Taiwan University campus, March 3, 1955, by Chen Hsien-Chen, the specimen seen to be phosphorescent at night; and one specimen taken in Hualien, September 8–10, 1955, by Chien, Feng, Ling and Wang.

6. *Mecistocephalus smithi* Pocock, 1895. One taken at Tsu-Yin, Hualien, by Tsai Chu and Ho Ming-Chuan in January, 1955; and two taken on Shih-Tou mountain, Hsin-Cho, by Tsai Chu-Fa, May 6, 1956.

7. *Mecistocephalus rubriceps* Wood, 1863. One taken on Shih-Tou mountain by Tsai Chu-Fa in January, 1955.

8. *Mecistocephalus punctifrons* Newport, 1845. One taken in Hualien by Tsai Chu-Fa in January, 1955.

9. *Mecistocephalus monticolens* Chamberlin, 1926. One taken in Hualien by Tsai Chu-Fa in January, 1955.

10. *Mecistocephalus mikado* Attems, 1928. Four taken at the Temple of Loyalty, Hualien, by Ho Ming-Chuan and Tsai Chu-Fa, in January, 1955.

11. *Mecistocephalus edentulus* Attems, 1928. One taken in Hualien by Tsai Chu-Fa in January, 1955.

12. *Pachymerium ferrugineum* Koch, 1855. Twelve specimens taken in Hualien by Tsai Chu-Fa in January, 1955.

Order Scolopendrida

13. *Scolopendra morsitans* Linné, 1758. One taken at Milan, Hualien, by Chien, Feng, Ling and Wang, September 8–10, 1955; two from Sa-Bo-Siang, Hualien, taken by Tsai Chu-Fa, January 31, 1955.

14. *Scolopendra subspinipes multidens* Newport, 1845. Two taken from Ta-Ru-Ko, Hualien, by Tsai Chu-Fa on February 3, 1956; fourteen taken at Milan, Hualien by Chien Taukiang Feng Chien Chow, Yin-Ling and Yu-Hsi Wang, September 8–10, 1955.

15. *Scolopendra subspinipes dehaani* Brandt, 1850. One from Chu-Yin, eighteen from the Temple of Loyalty, Hualien, by Tsai Chu-Fa and Ho Ming-Chuan in January, 1955.

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[1] This paper has also been published as follows:— Series 1e: Records of myriapods on Formosa with descriptions of new species. (2) *Quarterly Journal of the Taiwan Museum* 9(2): 155–159, 2 figs. 1956. The original descriptions of the genus *Chamberlinius* and the new pecies, *C. hualiensis* and *Rhysolus uraensis*, are included.

16. *Otostigmus aculeatus* Haase, 1880. Seventy-five taken from Hualien by Tsai Chu-Fa and Ho Ming-Chuan in January, 1955; one taken at Hot Spring, Taitung by Young Tsang-Tai.

17. *Otostigmus scaber* Porat, 1876. Seventeen from Hualien, taken by Ho, Chien, Feng, Ling and Wang in January and September, 1955.

18. *Otostigmus striatus* Takakuwa, 1940. One from Shih-Tou Mountain, Hsincho, by Tsai Chu-Fa, May 6, 1956.

19. *Rhysida longipes longipes* Newport 1844. Four from Taitung, taken by Young Tsang-Tai, August, 1955.

20. *Rhysida nuda brevicornuta* Wang, 1951. One taken at Taipei by Miss Chu Pao-Ching, May 22, 1956.

21. *Cryptops nigropictus* Takakuwa, 1940. One from Ta-Ru-Ko, Hualien, by Tsai Chu-Fa, February 3, 1956; one from Milan by Yu-Hsi Wang, September 8–10, 1956.

22. *Otocryptops sexspinosus* (Say), 1921. Four immature specimens from Sze-Tou Mountain, Hsin-Cho, taken by Tsai Chu-Fa, May 6, 1956.

ORDER LITHOBIIDA

23. *Bothropolys asperatus* Koch, 1878. Thirty-three from Hualien taken by Tsai, Ho, Chien, Ling, Feng and Wang, January and September, 1955.

24. *Chinobius chekianus* Chamberlin and Wang, 1952. Three taken in Hualien by Tsai Chu-Fa and Ho Ming-Chuan, January, 1955.

25. *Chinobius sachalinus* (Verhoeff), 1937. Four from Hualien, collected by Tsai Chu-Fa and Ho Ming-Chuan in January, 1955.

26. *Monotarsobius ramulosus* Takakuwa, 1941. Two taken in Hualien by Tsai Chu-Fa, January, 1955.

27. *Monotarsobius obtusus* Takakuwa, 1941. Two from Hualien, by Tsai Chu-Fa, January, 1955.

28. *Chinobius* sp. Nine immature specimens taken at Shih-Tou Mountain by Tsai Chu-Fa, May 6, 1956.

ORDER SCUTIGERIDA

29. *Thereupoda clunifera* (Wood) 1863. Two from Hualien in January, 1955 and two from Hsin-Cho, May, 1956, all small, taken by Tsai-Chu-Fa; one small and one 32 mm. long taken at Ta-Wu, Taitung, by Prof. Keng Hsuan.

Distributional Ecology of the Terrestrial Talitridae (Crustacea: Amphipoda) of Canada

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ABSTRACT

The known Canadian terrestrial amphipod fauna consists of twelve species of which Orchestia georgiana *and* Orchestoidea columbiana *are newly described. The regional and ecological distribution of the species is outlined and briefly related to morphological adaptations and to controlling and limiting effects of temperature, salinity, substratum, and other environmental factors.*

INTRODUCTION

The purpose of this paper is to delimit the geographical and ecological distribution of terrestrial amphipod crustaceans in Canada and to discuss their distribution in relation to controlling and limiting effects of certain environmental factors.

The present findings are based largely on collections from the Canadian Atlantic coast, 1950 to 1956 (Bousfield, 1952, 1955a, 1955b, 1956a, 1956b), and from the Canadian Pacific coast, 1955 (Bousfield, 1958). For additional records and material and other assistance the author is particularly grateful to Dr. J. F. L. Carl, Victoria, Mr. Terry Butler, Nanaimo, Dr. J. L. Barnard, Los Angeles, Mr. Glen B. Wiggins, Toronto, Mr. Pierre Brunel, Grande Riviere, Dr. Etienne Corbeil, Quebec, Dr. J. C. Medcof, St. Andrews, Mr. H. Squires, St. John's, Dr. E. Palmen, Helsinki, and many others.

The principal modifications accompanying the aquatic-terrestrial transition in amphipods are: (1) a reduction in size of gills and membranous body surfaces, (2) a strengthening of the urosome and ambulatory appendages for walking upright and hopping in the air medium, and (3) increasing efficiency of osmoregulation. In reduction of natatory appendages, tail fan, and sensory first antennae, and in several other respects, the body form has evolved to that of a generalized insect (MacIntyre, 1954). However, aquatic features that remain functional include the "carrying" habit in copulation, external fertilization, and the thoracic brood pouch. The body form of Canadian species may be classified as (1) the burrowing or substrate-modifying type (*Talorchestia*, *Orchestoidea*), and (2) the non-burrowing or non-modifying type (*Orchestia*, *Talitroides*). Species of the first type burrow in sand and shingle, aided by broad powerful bodies and relatively short, stout, heavily spinose appendages. Those of the second type are laterally compressed, relatively slender-legged, and adapted for hiding in the interstices of pebbles and debris of seashores, marshes, and woodlands.

SYNOPSIS OF THE SPECIES

Twelve terrestrial species of amphipods have been recorded from Canada and immediate territories; six from the Pacific coast, five from the Atlantic, and one from greenhouses in Ontario.

1. *Orchestia platensis* Kroyer 1844

Figs. 1c, 10b

Orchestia agilis S. I. Smith 1874.

Distribution. On the Canadian Atlantic coast (Fig. 1c):—

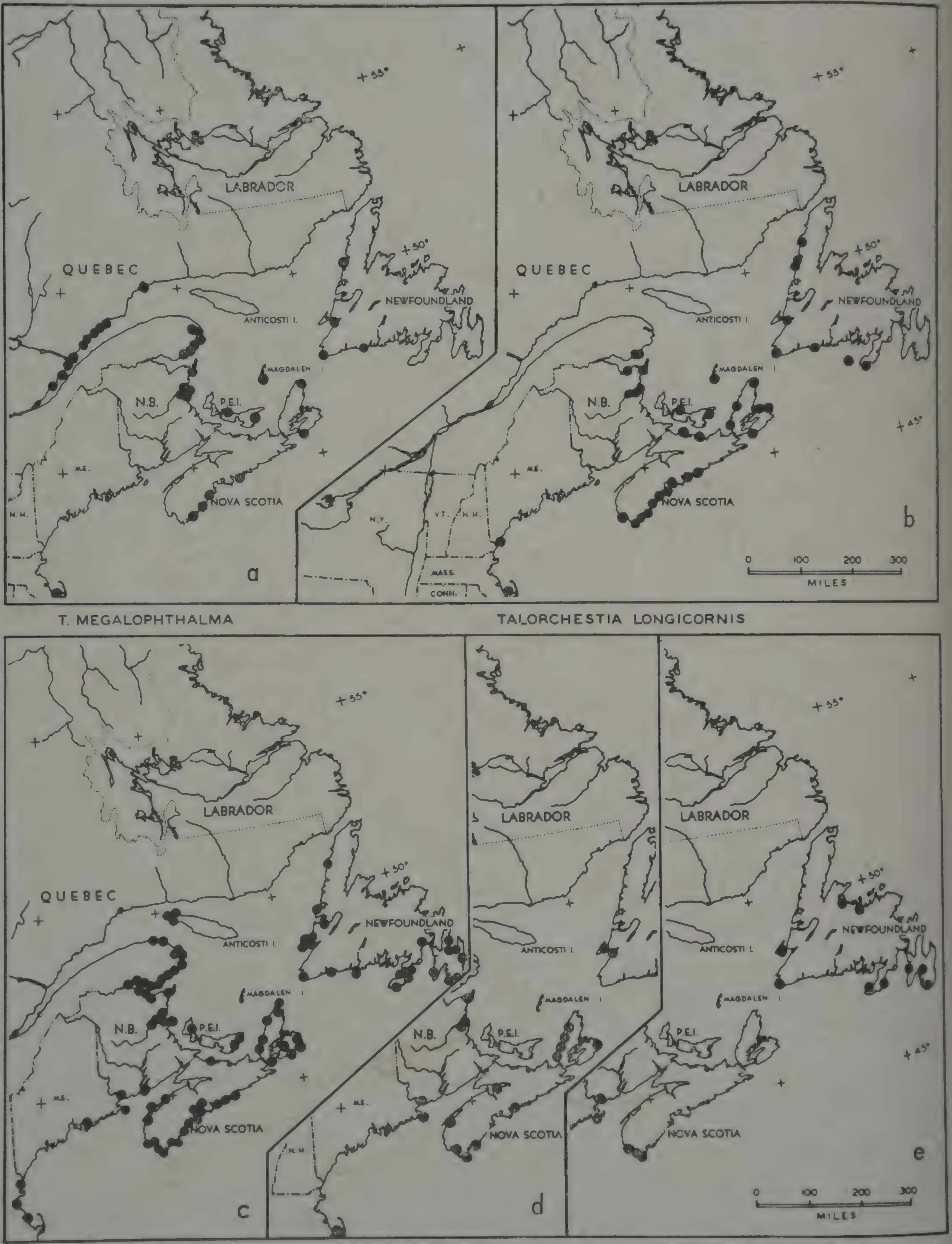
Newfoundland: west, south, and east coasts (Bousfield, 1956a); also taken by H. Squires in 1955 at Clarke's Beach, Avalon peninsula, and by E. Palmen in 1949 at Biscay Bay, Grand Bruit, Ramea I., Port-aux-Basques, and Port Saunders.

Quebec: Anticosti I. and Gaspe shores (Bousfield, 1955a) at St. Omer, Pt. Miguaska, Ste. Bonaventure, Paspebiac, St. Godfroy, Port Daniel, Gascons, Newport, Chandler, Ste. Adelaide, Little Pabos, Cap d'Espoir, Gaspe Bay, Petit Gaspe, Cap des Rosiers, Chloridorme, Grand Etang, Port Menier, Baie Ste. Claire, and Cap de Rabast.

New Brunswick: Miramichi estuary, several localities from the Gulf coast upriver to Newcastle (Bousfield, 1955b, Table IV); author collections, 1950, 1951, from Eel R., Youghall Beach, Petit Rocher, Shippigan, Tracadie, and Escuminac Pt., also St. John, St. Andrews, and Grand Manan.

Prince Edward Island: author collections, 1950, from Newport Ferry, Souris and Cascumpeque Bay.

Nova Scotia: Gulf coast, Cape Breton Island (Bousfield, 1956a) and western N. S. (Bousfield, 1956b); author collections, 1950, from Hampton Beach, Prim Pt., New Edinburgh, Argyle, and Sober I.; also, 1956, from Cape Fourchu (Yarmouth), Wedge Pt., Abbott Hbr., St. Anne Pt., Shag Hbr., Cape Sable I., MacLean I., Lockeport, Western Head (Liverpool), Spindler's Cove, Graves I., and Black Pt.


+55°
LABRADOR
QUEBEC
+50°
NEWFOUNDLAND
ANTICOSTI I.
MAGDALEN I.
N.B.
P.E.I.
ME.
N.H.
NOVA SCOTIA
a
N.Y.
VT.
MASS.
CONN.
+45°
b
0 100 200 300
MILES
c
d
e

T. MEGALOPHTHALMA

TALORCHESTIA LONGICORNIS

O PLATENSIS

O. GRILLUS

ORCHESTIA GAMMARELLA

Fig. 1. Distribution of terrestrial Talitridae. a, b, *Talorchestia* spp. c–e, *Orchestia* spp.

Habitat. Under stones, seaweed, logs, and debris, from well below to well above the high-water line of rocky, pebbly, sandy, and muddy shores. Scarce on sand, especially if *Talorchestia* present, and in salt marshes where *Orchestia grillus* dominates.

Remarks. A very hardy species, extending furthest northward (to Anticosti I. and nearly to Belle Isle Strait) of the non-burrowing species. Withstands the severe winter icing of the Gulf coast of Quebec and N. B. Not found along the St. Lawrence estuary, probably because of low summer water temperatures (7–10°C.).

2. *Orchestia grillus* Bosc 1802

Figs. 1d, 10c

Orchestia palustris S. I. Smith 1874.

Distribution. On the Canadian Atlantic coast (Fig. 1d):—

Newfoundland: St. George's estuary, Piccadilly (Bousfield, 1956a); collected by E. Palmen in 1949 at Stephenville Crossing and Piccadilly.

New Brunswick: author collections, 1950, 1951, from Shippigan, Miramichi Bay (Fox I., Egg I.,), Tidal Cove (Passamaquoddy Bay).

Nova Scotia: Several localities in Cape Breton Island (Shoemaker, 1930a, Bousfield, 1956a), Minas Basin (Tufts and Godfrey, pers. communic.), and St. Mary's Bay (Johansen, 1930); author collections in western Nova Scotia, 1956, at Eel Lake, Negro Hbr., MacLean I., and Cole Hbr.

Habitat. salt marshes; under half-dried *Fuci* and eel grass at and above the HW level, among roots of *Spartina* and other marsh grasses; muddy or sandy mud bottom; nest-building (Smallwood, 1905).

Remarks. Probably occurring in most of the salt marshes north to Chaleur Bay and Port-au-Port peninsula, but frequently overlooked because of its restricted habitat and secretive habits. Limited northward probably by deep frost and prolonged ice winters.

3. *Orchestia gammarella* (Pallas) 1766

Figs. 1e, 10a

Orchestia littorea Montagu 1808.

Distribution. On the Canadian Atlantic coast (Fig. 1e):—

Newfoundland: Notre Dame Bay, Port-au-Port, Burin and Avalon peninsulas (Bousfield, 1956a); collected by E. Palmen, 1949, at Placentia and Port-aux-Basques.

Nova Scotia: Argyle (Bousfield, 1956b); author collections in western Nova Scotia, 1956, at Wedge Pt., Ste. Anne Pt., and Abbott Hbr.

New Brunswick: author collections, 1951, at Tidal Cove; Machais Seal Islands, (Shoemaker, pers. communic.).

Habitat. Under stones, half-dried seaweed, debris, etc., at or above the HW level of rocky and stony beaches.

Remarks. The localities (above) are characterized by relatively mild winters with little or no shore ice action, by relatively humid and cool summers, and by high (>30°/₀₀) salinities. These conditions ensure the survival of non-hibernating shore animals such as *Orchestia gammarella*.

4. *Orchestia traskiana* Stimpson 1854

Figs. 2d, 10d

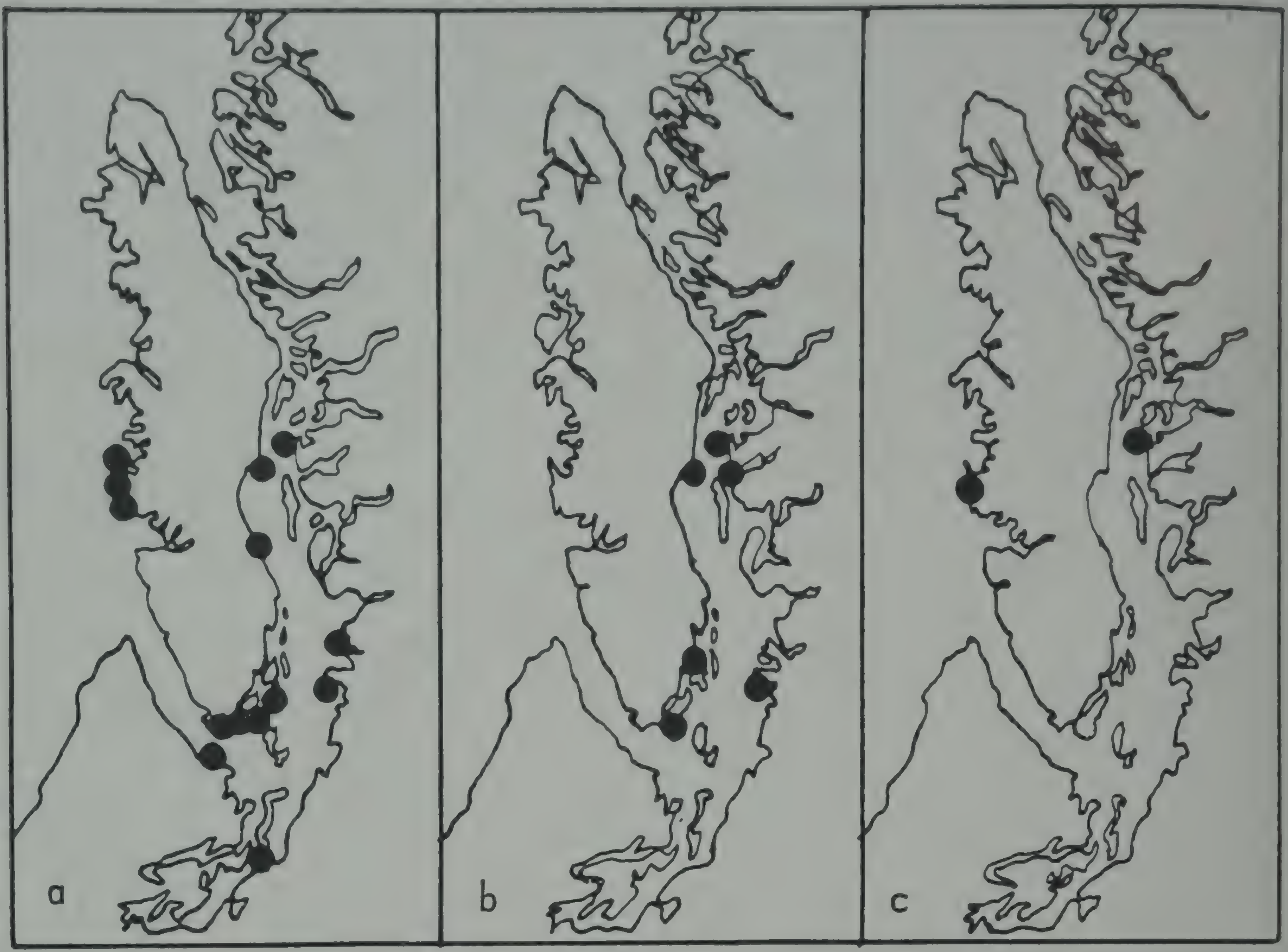
Distribution. On the American Pacific coast (Fig. 2d):—

British Columbia: CMNH collections from the Queen Charlotte Islands, June 28, 1934 (no other data); collected by Dr. J. F. L. Carl, Feb., 1956, at several localities around Victoria; author collections, 1955 (see Bousfield, 1958), at Clayoquot I., Tofino, Long Beach, Wreck Bay, Sooke, Witty's Lagoon, Albert Head, Cadborough Bay, Ladysmith Hbr., Chemainus Bay, Nanaimo, Nanoose Bay, Cottam Pt., Parkesville, Cape Lazo, Oyster R., Campbell R., Bloedel, Mittlenatch I., Savary I., Emmond's Beach, Kelly Bay, Spanish Banks, White Rock.

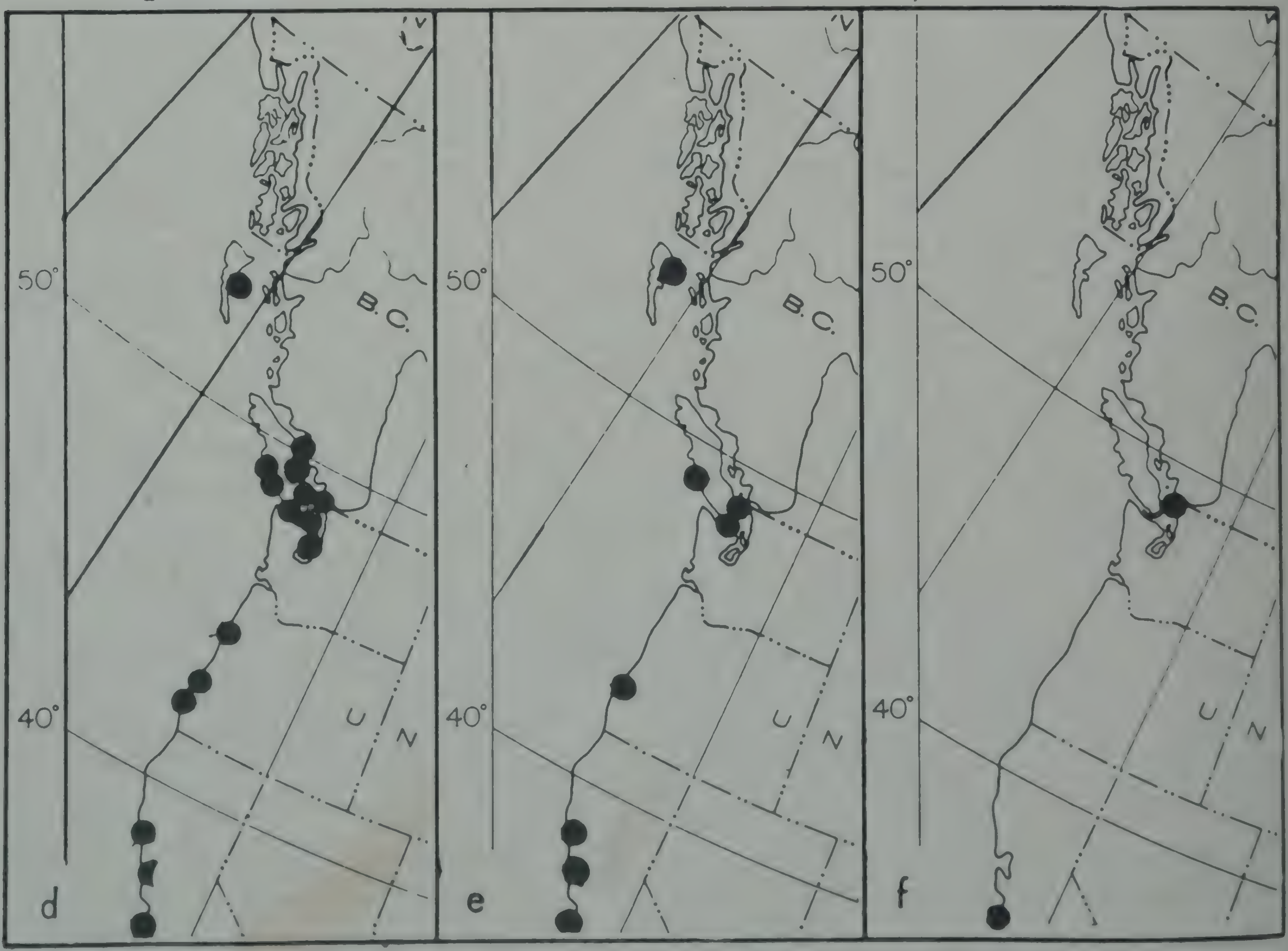
Washington: San Juan Islands (Thorsteinson, 1941); author collections, 1955, at Pt. Roberts; observed at Ediz Hook, Port Angeles.

Oregon: Coos Bay and Charleston (Barnard, 1954); collected by J. L. Barnard, March 16, 1956, at Newport.

Previously known from several localities in California.



O. pugettensis Orchestia georgiana O. columbiana



Orchestia traskiana O. californiana O. corniculata

Fig. 2. Distribution of terrestrial Talitridae. a, c, e, f, *Orchestoidea* spp. b, d, *Orchestia* spp.

HABITAT. Under stones, pebbles, half-dried *Fuci*, and eel grass on rocky, sandy, and muddy shores and in salt marshes.

REMARKS. A hardy species ranging from Lower California probably to Unalaska and tolerating a wide range of salinity. Closely related to the following species but distinguished by its larger size and more strongly plumose pleopods.

5. *Orchestia georgiana* n. sp.

Figs. 2b, 3, 10e

MALE. Eyes black, round, moderately large, near the anterior margin of the head. Antenna 1 extending slightly beyond fourth segment of peduncle of antenna 2, flagellum of five segments, shorter than peduncle. Antenna 2 relatively short, fourth (penultimate) segment of peduncle shorter than fifth, flagellum of 12–14 segments, slightly longer than peduncle. Mouthparts about normal. Maxilla 1, palp of outer plate very small, second joint minute. Maxillipeds, inner plate broadly rounded distally, bearing three heavy conical spine-teeth, the innermost smallest; palp of four distinct segments, the second with a broad median spinose lobe, and the fourth very small and armed distally with about six slender spines.

Gnathopod 1, side plate rounded below, ventrally spinose; coxa bearing a small median lobe, ventral margin lined with about eight long slender spines; segment 6 and dactyl forming a subchelate "hand"; prominent, minutely spinose "copulatory" lobes borne distally on the lower margin of segments 5 and 6 only. Gnathopod 2 large and powerful; sixth joint expanded, nearly as wide as long, upper margin smoothly convex, lower margin nearly straight and distally armed with 6–8 small spines, palm smooth, shallow convex, oblique, margin evenly armed with spines, posterior angle defined by two minutely spinose lobes, one prominent; dactyl heavy, smoothly curved, inner margin armed with minute spines, tip closing into a groove between the lobes of the posterior angle of the palm.

Peraeopods 1–5 typical of the genus, spines relatively short and blunt. Pleosome (metasome) side plate 1 rounded, a few small spines on the anterior margin; side plates 2 & 3, lower hind corner very slightly produced, hind margin of side plate 3 nearly straight, weakly serrate, armed with about 15 small spines. Pleopods, peduncle armed on outer margin with 3–5 spines and distally on the inner margin with a pair of minute "coupling" spines, rami subequal, 5–6 segmented, median and lateral margins lined with 6–12 plumose setae of varying lengths; pleopods 2 & 3 subequal, both longer than pleopod 1.

Urosome short, segments distinct; uropod 1 extending beyond uropod 2, lateral margins of rami armed with spines; uropod 3 very short, ramus shorter than peduncle, tapering more or less to a point, armed with 2–3 lateral spines and 3–4 terminal spines of unequal length. Telson a little longer than wide, ovate, with median posterior notch, outer margin armed with 8–12 prominent spines.

FEMALE. Generally smaller and less spinose than the male. Gnathopod 1 weakly subchelate, dactyl closing on a short oblique palm, tip extending well beyond the posterior angle of the palm. Gnathopod 2, margin of segment 5 smoothly convex above, almost straight below; segment 6 much shorter than 5, dropshaped, widest distally, weakly subchelate or almost chelate, expanded ventrally and distally into a tumid, finely spinulose lobe that extends beyond the short, obliquely closing dactyl. Margins of brood lamellae lined with about 30 long setae, each finely curled at the very tip.

Length: Male 12–16 mm., female 8–11 mm.

DISTRIBUTION. On the American Pacific coast (Fig. 2b):—

British Columbia: author collections, 1955, at Cadborough Bay, Victoria, August 15 (1♂); Chemainus Bay, V. I., July 29 (2♂♂); Cape Lazo, V. I. (TYPE LOCALITY), Aug. 12 (27♂♂, 19♀♀ (10 ovig.), 10 imm. (Paratypes)); Savary Island, Aug. 26 (32♂♂, 5♀♀, 1 juv.); Kelly Bay, Aug. 27 (2♂♂). Also: Savary I. (P.B.S. coll'n No. 7), Mar. 30/29 (8♂♂, 14♀♀ (ovig.)).

Washington: author collections, Aug. 29, 1955, at Pt. Roberts (8♂♂, 4♀♀).

HABITAT. Under stones, pebbles, driftwood and debris, particularly on a base of coarse sand or gravel, at the HW level.

REMARKS. All recorded localities are on the Strait of Georgia, hence the specific name. At certain stations (Cape Lazo, Savary I.) it was more abundant than *O. traskiana*. Compared with those of the outer coast and Strait of Juan de Fuca, surface temperatures are relatively high and salinities relatively low in the Strait of Georgia during the summer.

Orchestia georgiana is superficially similar to *O. ochotensis* Brandt (as described and figured by Gurjanova, 1951) but differs mainly in the structure of the gnathopods of both sexes and in the size, the former being much the smaller.

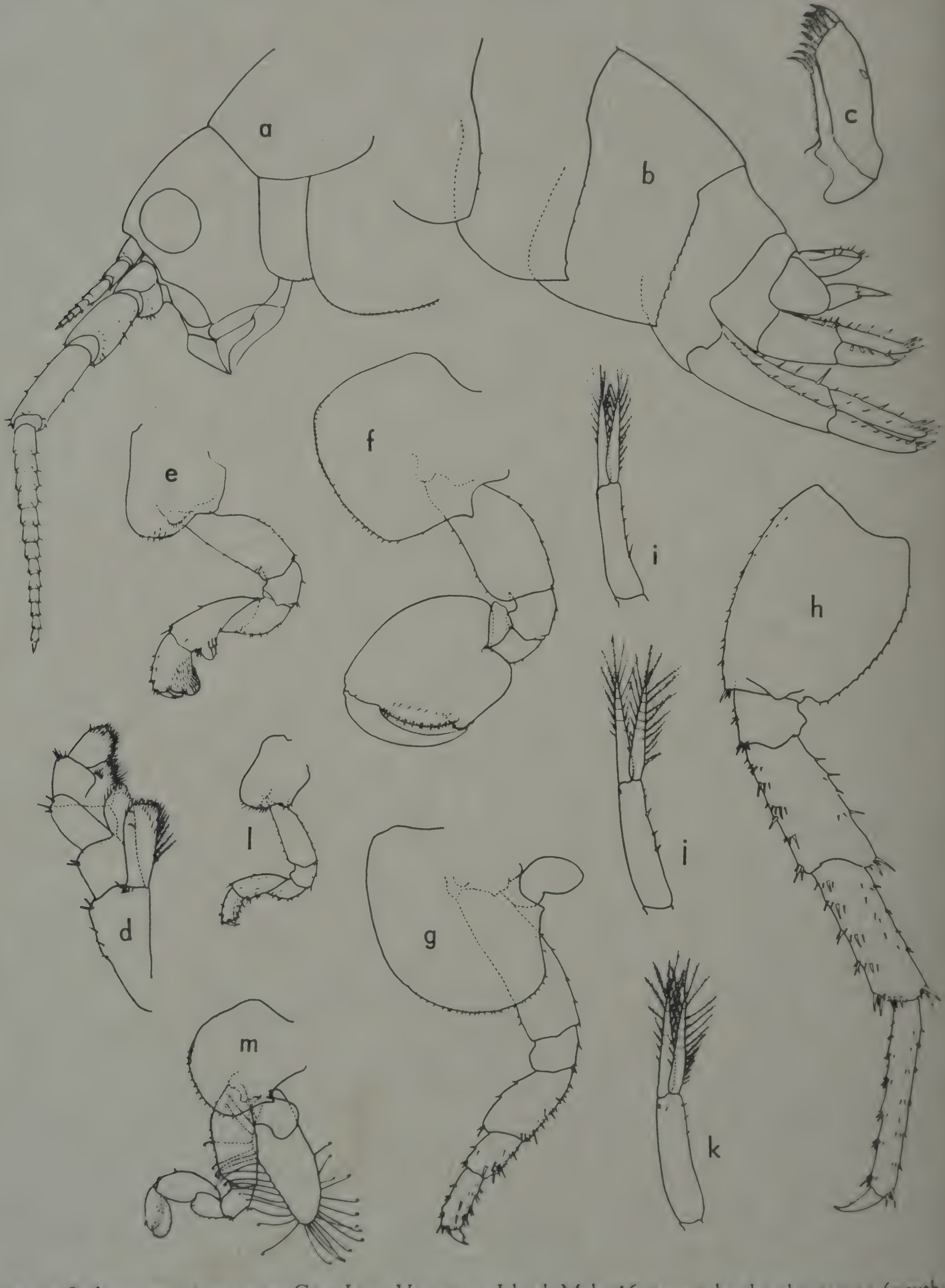


Fig. 3. *Orchestia georgiana* n. sp., Cape Lazo, Vancouver Island. Male, 16 mm.: a, head and antennae (mouthparts not complete). b, pleosome and urosome. c, maxilla 1. d, maxilliped. e, gnathopod 1. f, gnathopod 2. g, peraeopod 2. h, peraeopod 5. i, pleopod 1. j, pleopod 2. k, pleopod 3. Female, 11 mm.: l, gnathopod 1. m, gnathopod 2 and brood plate.

6. *Talitroides alluaudi* (Chevreux) 1896

Talitrus alluaudi (Medcof, 1939).
Talitrus (*Talitroides*) *alluaudi* (Hurley, 1955).

Distribution. Previously recorded in Canada from greenhouses in London and Toronto, Ontario (Medcof, 1939); not found in greenhouses in Victoria, Vancouver, and Halifax examined by the author in 1955.

Habitat. Under flower pots, debris, and in plant roots, usually associated with Oniscoidea, Chilopoda, Diplopoda, etc., in greenhouses of year-round warmth.

Remarks. Species of the genus *Talitroides* are morphologically, ecologically, and geographically distinct from the European-Atlantic *Talitrus saltator* (Pallas). Sub-adult stages of these two genera are quite unlike. The simple condition of the first gnathopod and the weakly subchelate condition of the second gnathopods in both sexes are the only traits shared by the adult stages of these genera. These characters are of specific value only and very probably afford an instance of parallel evolution in otherwise distantly related forms.

7. *Talorchestia megalophthalma* (Bate) 1862

Figs. 1a, 5b, 7, 9, 10g

Distribution. On the Canadian Atlantic coast (Fig. 1a):—

Newfoundland: Cape Ray and Stephenville Crossing (Bousfield, 1956a); collected by E. Palmen in 1949 at Burgeo and Stanford River.

Quebec: Magdalen Islands (Shoemaker, 1930a)?; Seven Islands (Bayne, 1908). Gaspe coast and north shore of the St. Lawrence Estuary (Bousfield, 1955a) at Newport, Newport Beach, Chandler, Barachois, Douglastown, Peninsula Gaspe, head of Gaspe Bay, Pt. Lebel, Pte-aux-Outardes, Bersamites, Islets de Jeremie, Portneuf, Pte Mille Vaches, Moulin-a-Baude, Baie Ste Catherine, St. Simeon, St. Joseph-de-la-Rive.

New Brunswick: author collections, 1951, at Shippigan, Miramichi Bay (Fox I., Vin I., Egg. I., Cheval Pt.), Escuminac.

Prince Edward Island: Souris Beach, A. Willey coll., Sept. 5–6, 1915,—1 male, 6 immatures; author observation at Cavendish Beach, July 14, 1950.

Nova Scotia: North Pond, Dingwall, and Michaud Pt., Cape Breton I., and Green Bay, Lunenburg Co. (Bousfield, 1956a); author collections in western N. S., 1956, at Lockeport, Summerville Beach, and Crescent Beach.

Habitat. Burrowing in sand or hiding beneath logs, algal debris, etc., up to the HW level of pure sandy beaches that are exposed to strong wave action. The young are diurnal and frequently hop about on the damp sand near the water line.

Remarks. The following morphological distinctions between *T. megalophthalma* and *T. longicornis* suggest that the former is less terrestrial and better adapted for aquatic life: pleopods much less reduced, antenna 2 shorter, and eyes larger. Where the species occur together, *T. megalophthalma* is closer to the water line and lives mainly in burrows, often six inches or more in depth, whereas *T. longicornis* may be found well above the HW level, does not usually burrow as deeply, and more often hides under logs, etc. *T. megalophthalma* is the only terrestrial species occurring well up the cold St. Lawrence estuary. The north side of the estuary is lined with suitable quartz-sand beaches of glacial and fluvial origin. The south shore has a few wave-deposited sandy beaches. For the most part, however, the sand is slatey, mixed with gravel, and otherwise unsuitable for the species.

8. *Talorchestia longicornis* (Say) 1818

Figs. 1b, 5a, 6–9, 10f

Distribution. On the Canadian Atlantic coast (Fig. 1b):—

Newfoundland: Burin peninsula, Miquelon?, Cape Ray, and Stephenville Crossing (Bousfield, 1956a); collected by E. Palmen in 1949 at Burgeo, Port-aux-Basques, Stephenville, Cow Head, Stanford R., and Port Saunders.

Quebec: Magdalen Islands (Shoemaker, 1930a); Port Daniel and East Port Daniel (Bousfield, 1955a).

New Brunswick: author collections, 1950, 1951, from Bass River (near Bathurst), Shippigan, Miramichi Bay (several localities from Fox I. upriver to Boishebert I., Bousfield, 1955b), and Escuminac.

Prince Edward Island: Souris Beach, A. Willey, 1915; author observation at Cavendish Beach, July 14, 1950.

Nova Scotia: Malagash Pt., Cape Breton Island (several localities), Clam Hbr. Cove, Lawrencetown (Bousfield, 1956a), Hunt's Point (Bousfield, 1956b); author collections, 1956, at Cape Fourchu (Yarmouth), Cape Sable I., Crane Pt., Round Bay, Lockeport, Port Mouton, Summerville, Crescent Beach, Hirtle Beach, Kingsburg, Spindler's Cove, Bayswater Beach; also Pictou, July, 1936, F. P. Ide.

Habitat. Burrowing in sand or under logs, detritus, etc., at and above the HW level of suitable sandy beaches of both outer coasts and estuaries.

Remarks. Probably limited northward by a combination of prolonged freezing winters and low summer water temperatures. Whereas *T. longicornis* stops far short of the northern limit of *T. megalophthalma* in the Gaspe and St. Lawrence estuary, further collecting is needed to establish their respective northern limits in the Belle Isle Strait region. Both species are rare in the Bay of Fundy owing to scarcity of suitable sandy beaches.

9. *Orchestoidea pugettensis* (Dana) 1855

Figs. 2a, 10i

Orchestoidea pugettensis Bate 1862.
Talorchestia tridentata Stebbing 1899.
non *O. pugettensis* Stebbing 1906.
O. pugettensis Thorsteinson 1941.

Distribution. On the American Pacific coast (Fig. 2a):—

British Columbia: author collections, 1955, at Clayoquot Sound, Long Beach, Wreck Bay, Witty's Lagoon, Albert Head, Cadborough Bay, Sidney Spit, Parkesville, Kyle Bay, Savary I., and Spanish Banks; collected by Dr. J. F. L. Carl, Feb., 1956, at Victoria Bay, Willows Beach, Cadborough B., Ross B., and in Aug. at Cabbage I.

Washington: Point Roberts (Thorsteinson, 1941); author collection, Aug. 29/55 at Pt. Roberts; observed July 11/55 at Ediz Hook, Port Angeles.

California: northern California (Stebbing, 1906)?

Habitat. Under logs, seaweed, debris, etc., or burrowing near the HW level of coarse sand or fine gravel.

Remarks. The species is closely related to *Orchestoidea corniculata* Stout 1913 and *O. benedicti* Shoemaker (1930b) both of which are more southerly in distribution. Dana's original description of the female, as quoted by Bate (1862), states: "inferior antennae not longer than half the body, flagellum hardly as long as base, the joints numerous, transverse . . ", and "length eight lines", and habitat "Puget's Sound". These features were (and still are) specifically distinctive. However, Stebbing's description of a female *Orchestoidea* (1906, p. 529) is very probably that of *O. californiana* and cannot be Dana's *O. pugettensis* since he states: "antenna 2, flagellum rather longer than peduncle, of 30 joints . ". Stebbing's description of *Talorchestia tridentata* (1899) is clearly applicable to the male of *O. pugettensis* as described by Thorsteinson (1941). The fact that a student of Stebbing's experience could interpret gnathopod 1 of the male to be subchelate renders highly questionable the generic value of the apical pellucid process of segment 6 alone.

10. *Orchestoidea corniculata* Stout 1913

Figs. 2F, 10h

Distribution. On the American Pacific coast (Fig. 2f):—

Washington: Point Roberts (Thorsteinson, 1951).

California: Laguna Beach (Stout, 1913).

Habitat. Burrowing near the HW level of beaches of sand and fine gravel, mainly in estuaries where salinities are reduced.

Remarks. Not found in limited collections made at Pt. Roberts by the author in 1955.

11. *Orchestoidea columbiana* n. sp.

Figs. 2c, 4, 10k

Male (11 mm. instar). Eyes large, black, subrotund, width more than half that of head, front margin nearly straight, hind margin more rounded. Antenna 1 reaching about middle of segment 4 of peduncle of antenna 2, flagellum much shorter than the peduncle and consisting of 5–6 short segments, the last very small. Antenna 2, segment 5 of peduncle about twice the length of segment 4, flagellum of at least 20 segments, longer than peduncle; basal segment of peduncle (fused to head) spinose in front. Mouthparts about normal. Maxilla 1, palp of outer plate very small, 2-jointed, outer joint minute. Maxillipeds, inner plate expanding distally, broadly rounded or nearly truncate, margin armed with three conical spine-teeth; palp of three prominent segments, each broadly expanded, and a minute rudimentary 4th segment near the tip of the 3rd (not shown in Fig. 4).

Gnathopod 1 simple; antero-ventral angle of side plate nearly a right angle; coxa bearing a small median lobe, ventrally armed with 7–9 longish spines; segment 5 bearing distally on lower margin a prominent "copulatory" lobe; segment 6 shorter than 5, bearing distally on ventral margin a low rounded lobe against which the basal portion of the long dactyl closes, thus appearing weakly subchelate. Gnathopod 2, segment 4 with weakly chitinized posterior lobe; segment 6 large and powerful, oval, upper margin convex and smooth, lower margin convex and armed with spines; palm evenly convex, very oblique, regularly spinose, demarcated from lower margin by two or three blunt spine-teeth against which closes the tip of the smoothly curving dactyl.

Peraeopods typical of the genus, heavily spinose; segment 2 of P5 more widely expanded than that of P4.

Pleosome (metasome), side plates 1–3, anterior and ventral margins smooth, lower posterior corner slightly produced into short acute points, posterior margins of 2 & 3 armed with a few minute spines. Pleopods 1–3 successively decreasing in size; peduncle armed on both margins with spines and distally on the inner margin with a pair of minute "coupling" spines; rami of each pleopod subequal, outer ramus of pleopods 2–3 longer than inner, all but the terminal segments fused, each ramus armed distally with 5–6 plumose setae and proximally on outer margin with a variable number of spines.

Urosome segments partly coalesced dorsally. Uropod 1 strongly spinose, rami extending beyond those of uropod 2; uropod 3, ramus longer than peduncle, rounded at the tip, multispinose. Telson short, spade-shaped, about as wide as long, slightly notched at the apex, with several stout spines on upper surface.

FEMALE. Eyes somewhat smaller and flagellum of antenna 2 with fewer segments. Gnathopod 1 simple, similar to that of male except without rounded lobes on lower margins of segments 5 and 6. Gnathopod 2, anterior and posterior margins of segment 2 lined with small spines; segment 4 with prominent, weakly chitinized posterior lobe; segment 5, lower margin sligthly concave, distal angle sharp; segment 6 as long as segment 5, widest at the middle, lower margin evenly convex, ventral lobe produced well beyond tip of minute dactyl.

Length: Male 11mm., female 13–15 mm.

DISTRIBUTION. On American Pacific coast (Fig. 2c):—

British Columbia: author collections, 1955, at Long Beach, Wickaninnish Bay (TYPE LOCALITY), Aug. 2—1 male holotype (11 mm.), 1 female allotype (13 mm.), 4 immature and 31 juvenile paratypes. Savary Island, Strait of Georgia, Aug. 26–2 females (non-ovig.).

HABITAT. At or below the high-water level of sandy beaches.

REMARKS. The species is known only from the coast of British Columbia, hence the specific name. The minute rudimentary 4th joint of the maxilliped palp is also present in *O. pugettensis*, *O. corniculata*, and is extremely minute in *O. californiana*. The American-Pacific genus *Orchestoidea* is evidently more terrestrial than the American-Atlantic genus *Talorchestia* in greater reduction of antenna 1 and pleopods and weaker development of copulatory tubercles on gnathopod 1 of the male, among other characteristics. Based on morphological evidence, *O. columbiana* is less terrestrial than *O. californiana*. This pair appears to be ecologically and morphologically parallelled on the Canadian Atlantic coast by *Talorchestia megalophthalma* and *T. longicornis* respectively.

12. *Orchestoidea californiana* (Brandt) 1851

Figs. 2e, 10j

DISTRIBUTION. On the American Pacific coast (Fig. 2e):—

British Columbia: author collections, 1955, at Clayoquot I., Long Beach, Witty's Lagoon, Cadborough Bay, and Sidney Spit; collected by Dr. J. F. L. Carl on June 8/56 at

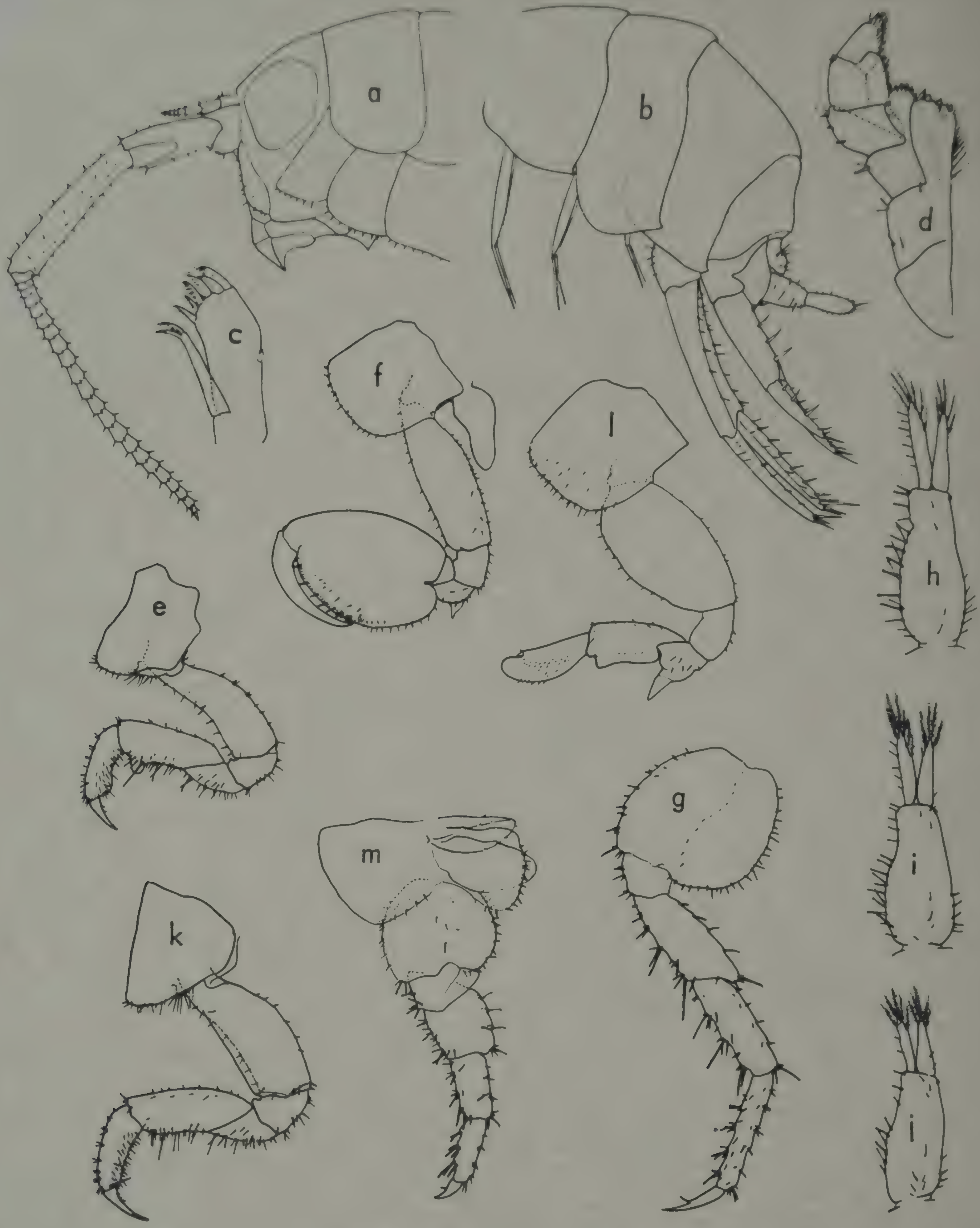


Fig. 4. *Orchestoidea columbiana* n. sp. Long Beach, Vancouver Island. Male, 11 mm. instar: a, head and antennae. b, pleosome and urosome. c, maxilla 1. d, maxilliped. e, gnathopod 1. f, gnathopod 5. g, peraeopod 5. h, pleopod 1. i, pleopod 2. j, pleopod 3. Female, 13 mm.:k, gnathopod 1. l, gnathopod 2. m, peraeopod 3 and brood plate.

Cadborough Bay and on Aug. 26/56 at Sidney Spit; also CMNH material from Long Beach, V. I., John Macoun, 1909.

Washington: beaches of Puget Sound, upper littoral (Thorsteinson, 1941).

Oregon: Charleston, Coos Bay (Barnard, 1954).

California: author collection, July, 1955, at Dillon Beach, Tomales Bay; also collected by Dr. J. L. Barnard, Mar. 31/47, at Piedras Blancas, and Dec. 27/55 at Pismo Beach.

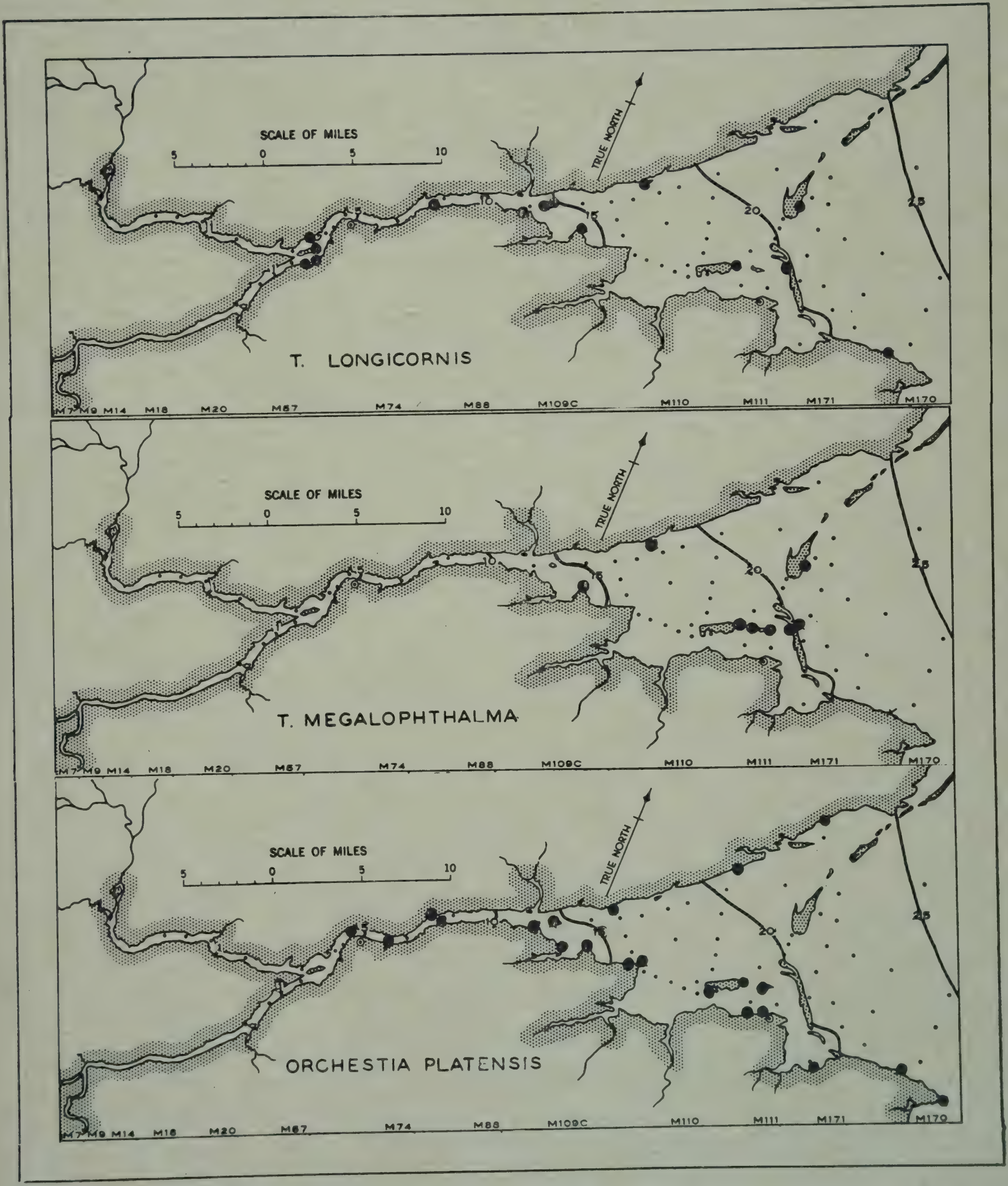
HABITAT. Burrowing in the substratum or under logs, etc., at or about the HW level of fine sand beaches of surf-exposed coasts; not in estuaries where summer salinities are less than about 28°/₀₀.

REMARKS. Of these four species of *Orchestoidea* the spinose armature of the abdominal side plates is strongest and the number of natatory setae on the pleopods is least in *O.*

californiana. The fact that this relationship holds even in quite immature specimens of each species indicates that *O. californiana* is the most terrestrial of the group.

LOCAL DISTRIBUTION

Being amphibious animals the beach fleas respond to factors of both marine and terrestrial environments. The ecology and behaviour of these animals have been studied by Reid (1947) and Williamson (1951) in Britain, Smallwood (1903, 1905) and Edwards and Irving (1943) in America, and MacIntyre (1954) in New Zealand. Their results indicate that important controlling factors of the marine environment are water salinity, particularly of interstitial water of the burrows, and water temperature, critical for survival and reproduction in this essentially warm-stenothermal group. Important limiting factors of the terrestrial environment are the compactness and nature of the substratum (sand, gravel,


T. LONGICORNIS

T. MEGALOPHTHALMA

ORCHESTIA PLATENSIS

Fig. 5. Distribution of terrestrial Talitridae in the Miramichi estuary, N.B., in relation to mean surface salinity. a, b, *Talorchestia* spp.

shingle, etc.), the depth of ice formation (frost penetration) and the duration of winter. For instance, temperatures in burrows of *T. megalophthalma* surviving the winter did not fall below 3°C. (Edwards and Irving, 1943). In summer, temperatures at the surface of the sand may reach 55°C, but in the burrows seldom exceed 23°C. The animals are unable to survive indefinitely in dry air (relative humidity 40–70%) unless supplied with moist food. During daylight hours they hide in burrows where relative humidity is 90–100%. Orientation of the animals on the beach is both geotropic and visual and is also controlled by memory. Their numbers are controlled chiefly by predatory flies, beetles, spiders, centipedes, and birds, etc., and by parasites, notably the biting mite *Thinoseius* which clusters on the legs and under the thorax.

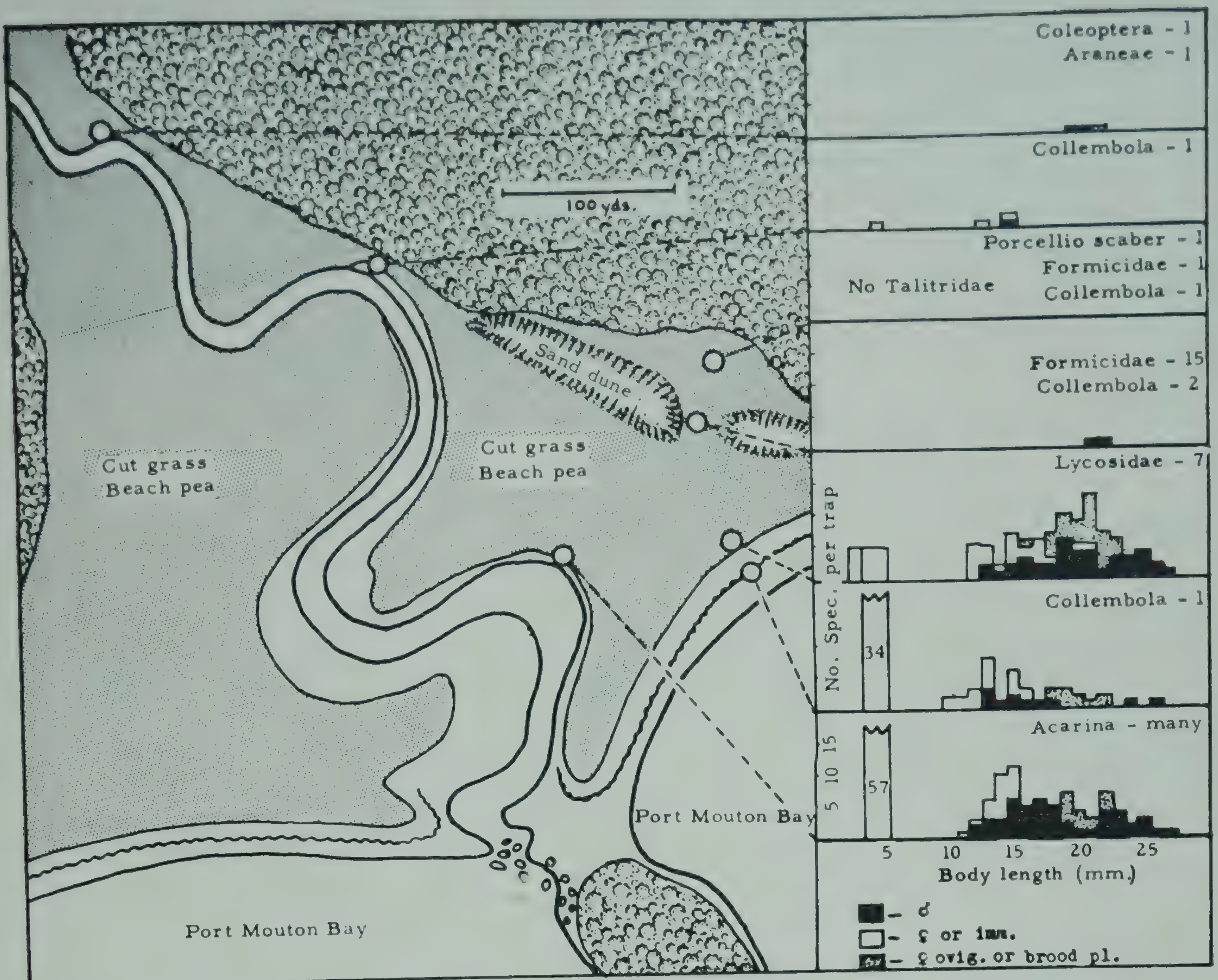
The local occurrence of certain species on Canadian Atlantic beaches illustrates the manner in which environmental factors may control distribution. Fig. 5 shows the distribution of *Talorchestia longicornis*, *T. megalophthalma*, and *Orchestia platensis* in the Miramichi estuary during 1951 in relation to the mean summer surface salinity. Of the burrowing forms, *T. longicornis* penetrates upriver to Nelson and Boishebert Island where the salinity value is only 3°/$_{oo}$, frequently falling to 0°/$_{oo}$ during freshets. The less terrestrial *T. megalophthalma* is limited landward at 14°/$_{oo}$ (at Baie St. Paul, the landward limit in the St. Lawrence estuary, the summer salinity is 17°/$_{oo}$). The non-burrowing *O. platensis* stops at Newcastle and a salinity of about 5°/$_{oo}$.

Fig. 6 shows the population composition of *T. longicornis* at various distances inland from the mouth of the small south-west Port Mouton estuary, Nova Scotia, in mid-July, 1956. Salinities at the mouth varied from 30°/$_{oo}$ at HW to about 5°/$_{oo}$ at LW and 700 yards (700 meters) upstream from 15°/$_{oo}$ at HW to 0°/$_{oo}$ at LW. The population was sampled at seven localities by setting out shallow pans, each six inches in diameter, into which the nocturnally roving animals chanced to fall.

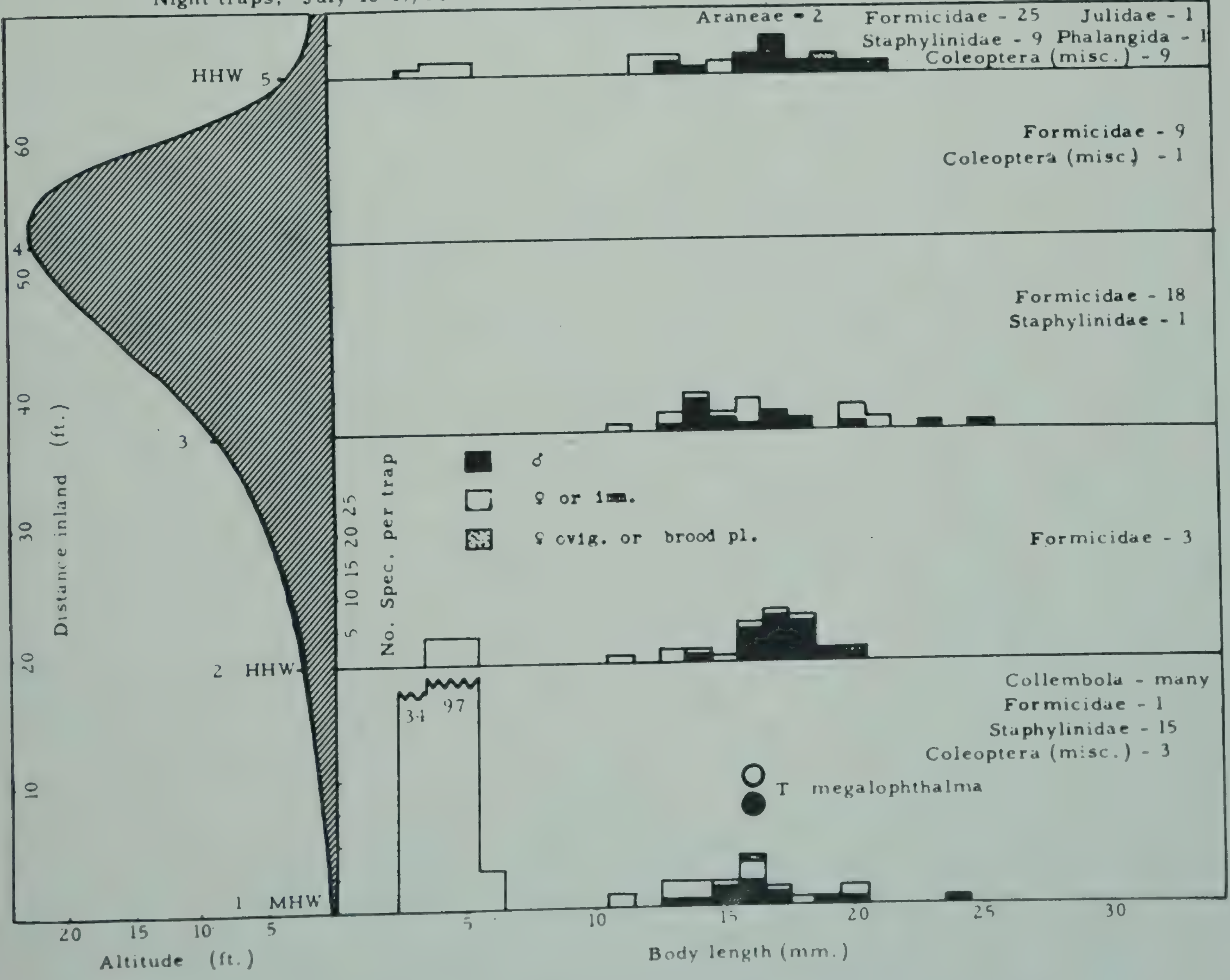
T. longicornis burrows in the sand throughout the region of cut grass and beach pea. Adults or sub-adults occur more than 100 yards from the water's edge, associated with spiders, ants, and other terrestrial arthropods, but do not reach the forest border. Only within 10 yards of the HW line may be found sizeable populations and populations containing ovigerous females and newly hatched young. These last live in shallow pits in the damp sand by day. The life cycle is normally complete in one year. The shoreline population is composed of very small individuals (3–6 mm.) hatched during the spring and early summer of the present year, sub-adults (10–17 mm.) born during the previous summer and fall, and fully mature adults (18–27 mm.) born the previous spring and early summer.

The results of other night samples in southwestern Nova Scotia during 1956 illustrate the importance of the slope of the beach on the composition of the population and on the degree of penetration landward from the shoreline, and vertically above the HW level. Fig. 7 shows the distribution of *Talorchestia* spp. on both sides of Crescent Beach bar on a moonlit night of mid-July, 1956. Only the outer side is exposed to strong wave action and then only from the south-west. Below the dune proper the outer slope is relatively steep (15–20%). The sand is of fine white quartz. The entire population of *T. longicornis* is restricted horizontally to within 40 feet (13 meters), and vertically to within 12 feet (4 meters) of the mean high water level. The young-of-the-year occur abundantly only at or below the MHW level. Strictly terrestrial arthropods are most abundant in the wave-cast debris between mean high water and higher high water levels, but a small red ant prefers the dune proper. *T. megalophthalma* (1 male, 1 female) occurred only at the MHW level of the outer beach.

Fig. 8 shows the distribution of *T. longicornis* on the semi-protected sand beach at Kingsburg on a foggy night near the end of July, 1956. The slope is moderately steep (about 15%) and the sand is of metamorphic origin and dark in colour. Only *T. longicornis* was taken. The species occurred at all four locations, even in the sand vegetation beyond the crest of the dune and 11 feet above the MHW level. The bulk of the population, especially large males, was concentrated in the debris zone. On this date relatively few ovigerous females and brood young, but more 4th and 5th instars, were present. Smallest instars (3–5 mm.) were nearest the water's edge, but some of the older and larger (6–8 mm.) instars were well above the HHW level. A few other terrestrial arthopods were found on the dune.

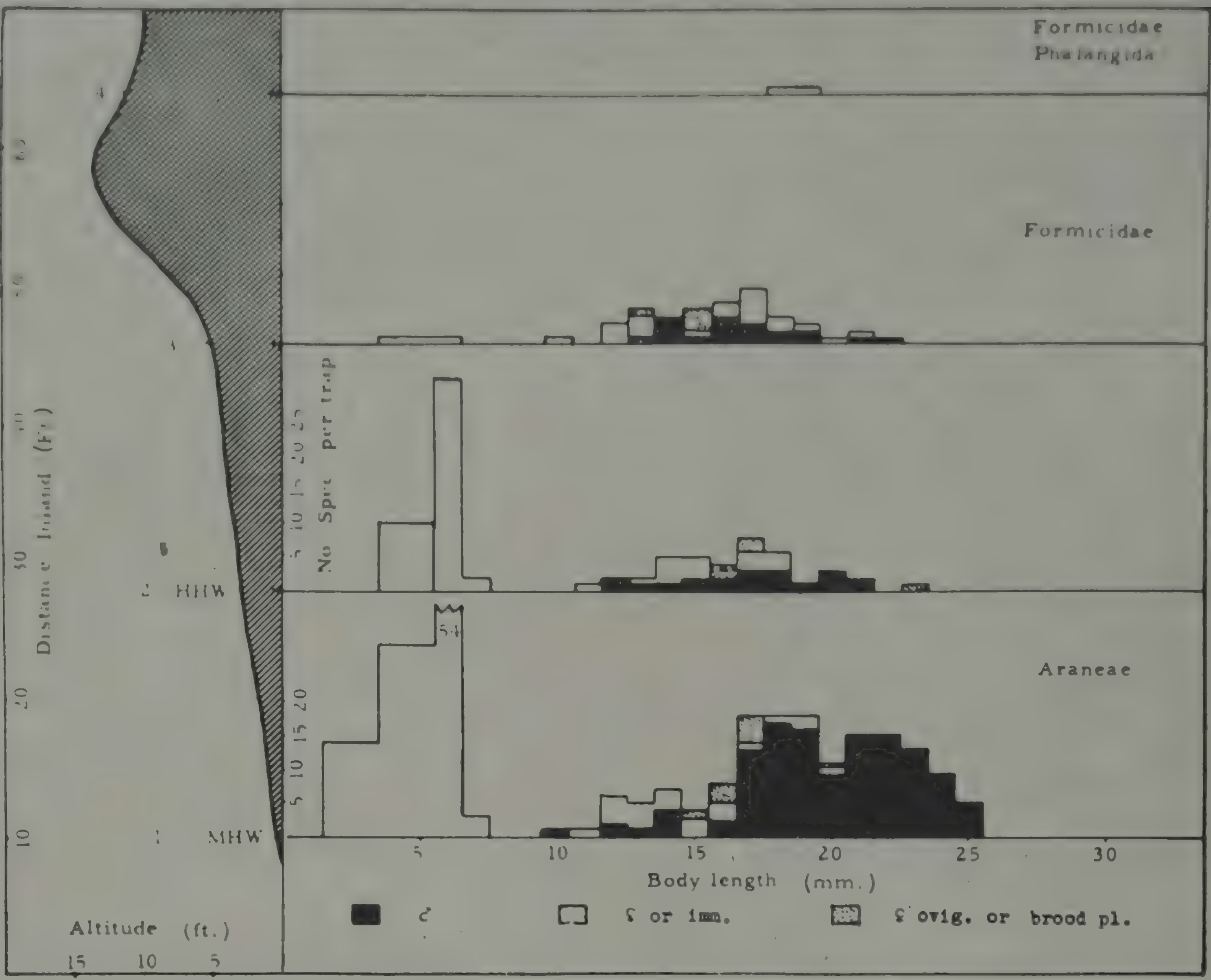

Coleoptera - 1
Araneae - 1
Collembola - 1
Porcellio scaber - 1
Formicidae - 1
Collembola - 1
No Talitridae
Formicidae - 15
Collembola - 2
Lycosidae - 7
Collembola - 1
Acarina - many
No. Spec. per trap
5 10 15
34
57
5 10 15 20 25
Body length (mm.)
■ – ♂
☐ – ♀ or imm.
▨ – ♀ ovig. or brood pl.
100 yds.
Sand dune
Cut grass
Beach pea
Cut grass
Beach pea
Port Mouton Bay
Port Mouton Bay

Distribution of Talorchestia longicornis in the South-west Port Mouton estuary, Queens Co., N. S., Night traps, July 18-19/56. Moonlight; LW - 12:47 a.m. HW - 6:45 a.m.



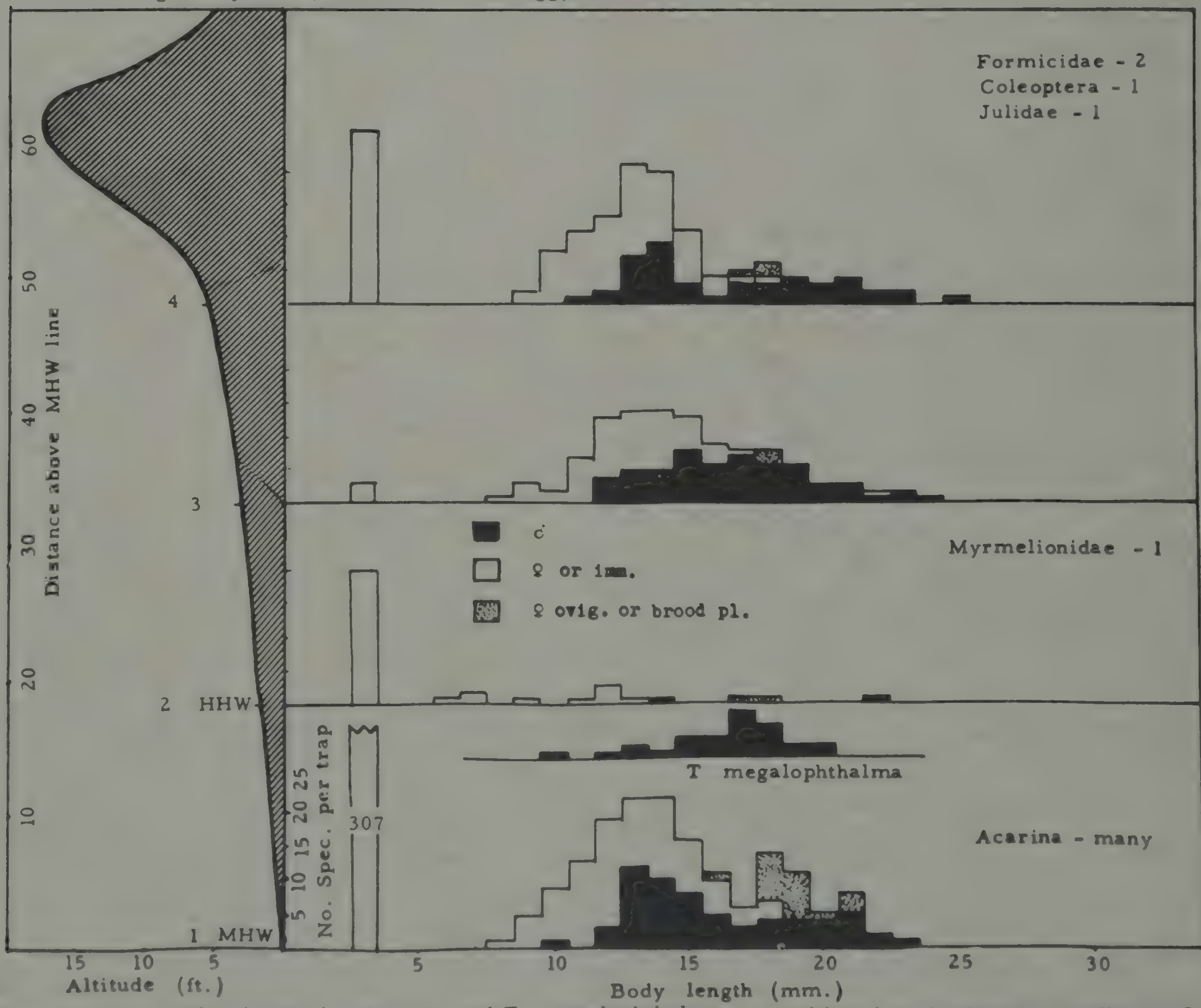
Distribution of T. longicornis and T. megalophthalma on Crescent Beach, Lunenburg Co., N. S. Night traps, July 19-20/56. Moonlight; LW - 12:55 a.m. HW - 7:30 a.m. ADST

Figs. 6, 7. Distribution of *Talorchestia* spp. as indicated. Fig. 6, upper. Fig. 7, lower.



Distribution of T. longicornis on sand beach at Kingsburg, Lunenburg Co., N. S.

Night traps, July 26-27,/56. Foggy LW - 5:31 a.m. HW - 11:23 p.m.



Distribution of Talorchestia longicornis and T. megalophthalma on sand beach at Lockeport, Shelburne Co N. S., Night traps, July 3-4/56. Moonlight; LW - 11:10 p.m. HW - 4:53 a.m.

Figs. 8, 9. Distribution of *Talorchestia* spp. as indicated. Fig. 8, upper. Fig. 9, lower.

Fig. 9 shows the distribution of *Talorchestia* spp. on a wave-exposed sand beach at Lockeport on a moonlit night in late June, 1956. The slope is relatively gentle (about 10%)

and the sand is of fine white quartz. *T. longicornis* occurred from MHW level to the base of the dune (altitude 7 feet) whereas *T. megalophthalma* was taken only at the MHW level. The former population contained sexually mature adults, sub-adults, and brood young, whereas the latter consisted only of males, mostly mature. Discarding the results of trap No. 2, which proved not deep enough to retain most specimens, the population of *T. longicornis* was fairly constant at all levels sampled. Newly hatched young were numerous nearly 50 feet above the MHW line. However, the altitude here is only 5–6 feet and damp sand is close to the surface owing to the very gentle slope of the beach. The scarcity of other terrestrial invertebrates, except on the dune proper, is attributable to the exposed wind-swept location of the beach.

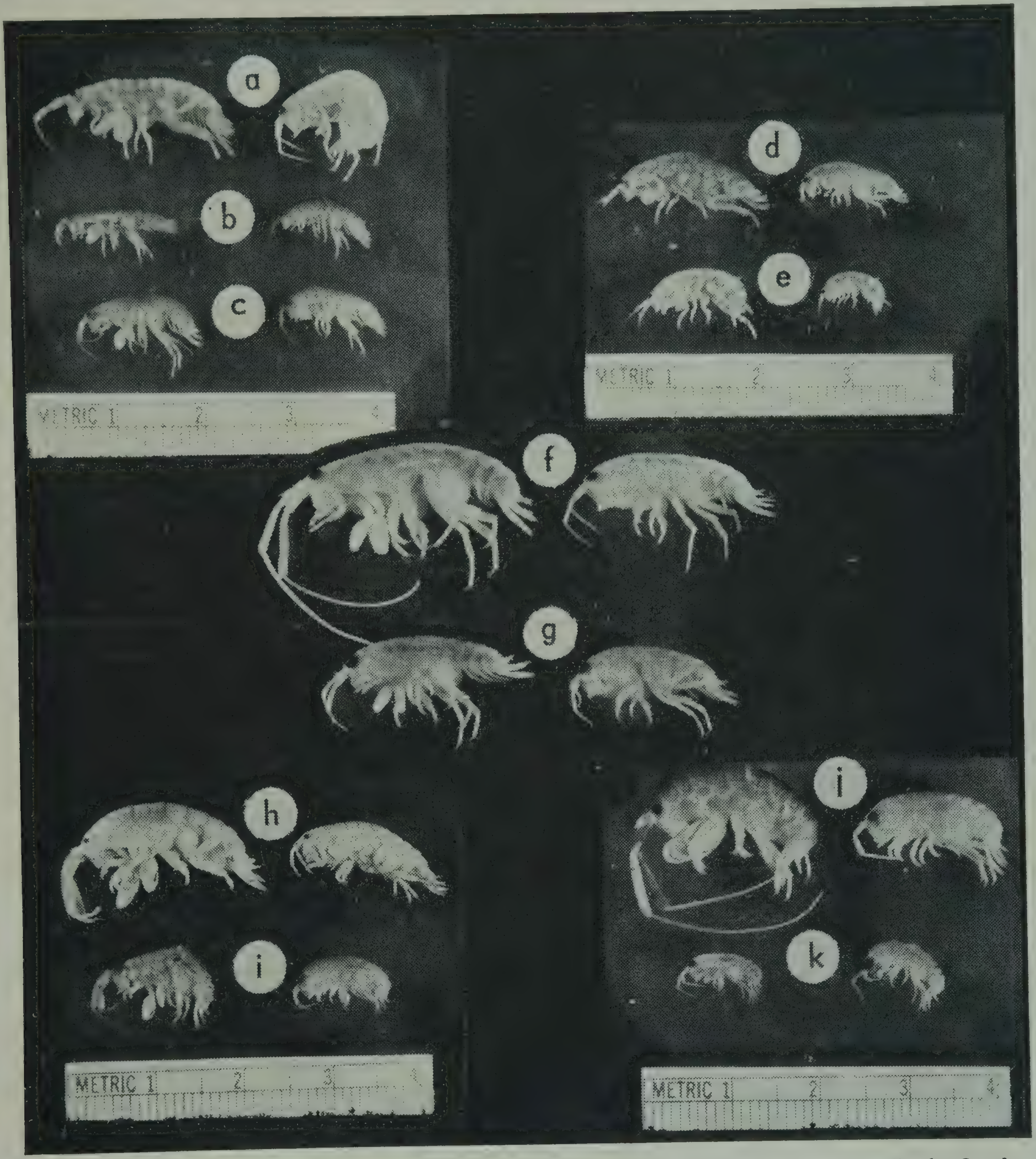


Fig. 10. Canadian terrestrial Talitridae, male on left, female on right. a, *Orchestia gammarella*. b, *O. platensis*. c, *O. grillus*. d, *O. traskiana*. e, *O. georgiana*. f, *Talorchestia longicornis*. g, *T. megalophthalma*. h, *Orchestoidea corniculata*. i, *O. pugettensis*. j, *O. californiana*. k, *O. columbiana*.

SUMMARY AND CONCLUSIONS

1. The geographical distribution and habitat preference of terrestrial and semi-terrestrial amphipod crustaceans in Canada are outlined.

2. Of the twelve known Canadian Talitridae, *Orchestia georgiana* and *Orchestoidea columbiana* are herewith newly described.

3. *Talorchestia longicornis* tolerates lower salinities, lives at higher levels on the beach, and extends further inland than the morphologically more aquatic *T. megalophthalma*.

4. *Talorchestia megalophthalma* extends further northward in the St. Lawrence region of the Canadian Atlantic coast than does *T. longicornis*. By virtue of deeper burrowing and more aquatic habits *T. megalophthalma* presumably better withstands the distributionally limiting effect of winter frost in the tidal zone.

5. Depending largely on the slope of the beach, adults and sub-adults of *T. longicornis* may occur more than 100 yards (100 meters) inland and more than 10 feet (3 meters) above the higher high water level, whereas the newly hatched young are restricted to the immediate shore line.

REFERENCES

Barnard, J. L. 1954. Marine Amphipoda of Oregon. *Oregon State Monographs, Studies in Zoology*, No. 8: 37 pp., 33 pl.

Bate, C. S. 1862. Catalogue of the amphipodous Crustacea in the British Museum. *Taylor and Francis*, London, 399 pp., 58 pl.

Bayne, P. M. 1908. Crustacea collected at Seven Islands, Quebec. M. A. Thesis, Dept. Zool., Univ. Toronto. (Unpublished).

Bousfield, E. L. 1952. Zoological investigations in the Maritime Provinces. *Bull. Nat. Mus. Canada* 126: 188–194.

Bousfield, E. L. 1955a. Studies on the shore fauna of the St. Lawrence estuary and Gaspe coast. *Bull. Nat. Mus. Canada* 136: 95–101.

Bousfield, E. L. 1955b. Ecological control of the occurrence of barnacles in the Miramichi estuary. *Bull. Nat. Mus. Canada* 137: 69 pp.

Bousfield, E. L. 1956a. Studies on the shore crustacea collected in eastern Nova Scotia and Newfoundland, 1954. *Bull. Nat. Mus. Can.* 142: 127–152.

Bousfield, E. L. 1956b. Malacostracan crustaceans from the shores of western Nova Scotia. *Proc. N. S. Inst. Sci.* 24(1): 25–38, 3 figs.

Bousfield, E. L. 1958. Ecological investigations on shore invertebrates of the Pacific Coast of Canada. *Bull. Nat. Mus. Canada.* 147: 104–115.

Edwards, G. A., and L. Irving. 1943. The influence of temperature and season upon the oxygen consumption of *Talorchestia megalophthalma*. *Jour. Cell. & Comp. Physiol.* 21: 183–189.

Gurjanova, E. F. 1951. Amphipoda (Gammaridea) of the seas of the USSR and adjoining waters. *Trans. Zool. Inst., Akademia Nauk* 41: 1029 pp.

Holmes, S. J. 1904. The Amphipoda of southern New England. *Bull. U. S. Bur. Fish.* 24: 457–529.

Hurley, D. E. 1955. Studies on the New Zealand amphipodan fauna. No. 8. Terrestrial amphipods of the genus *Talitrus* Latr. *Pacific Science*, April, 1955: 143–157.

Johansen, F. 1930. Marine Crustacea, Malacostraca, and Pantopoda (Pycnogonida) collected in the Gulf of St. Lawrence, Newfoundland, and the Bay of Fundy in 1919, 1922, 1923, 1925, and 1926. *Canadian Field-Naturalist* 64(4): 91–94.

MacIntyre, J. 1954. A common sand hopper. M. A. Thesis, U. of Auckland. (Unpublished).

Medcof, J. C. 1939. Additional records of the terrestrial amphipod, *Talitrus alluaudi* Chevreux in N. America. *Amer. Midl. Nat.* 22(1): 216–217.

Reid, D. M. 1947. Talitridae (Crustacea: Amphipoda) Synopses Brit. Fauna. *Linn. Soc. Lond.* No. 7: 25 pp.

Shoemaker, C. R. 1930a. The amphipods of the Cheticamp Expedition of 1917. *Contr. Can. Biol. & Fish.* 5(10): 221–359.

Shoemaker, C. R. 1930b. Descriptions of two new amphipodous crustaceans (Talitridae) from the United States. *J. Wash. Acad. Sci.* 20(6): 107–114.

Smallwood, M. E. 1903. The beach flea: *Talorchestia longicornis*. Brooklyn Inst. Arts & Sci., *Cold Spring Harbor Mon.* II: 21 pp., 2 pl.

Smallwood M. E. 1905. The salt-marsh amphipod: *Orchestia palustris*. Brooklyn Inst. Arts & Sci., *Cold Spring Harbor Mon.* III: 27 pp., 3 pl.

Stebbing, T. R. R. 1906. Amphipoda; I Gammaridea. *In* Das Tierreich, Berlin, 784 pp.

Thorsteinson, E. D. 1941. New or noteworthy amphipods from the North Pacific coast. *Univ. Wash. Publ. in Oceanography* 4(2): 50–96, 8 pl.

Williamson, D. I. 1951a. On the mating and breeding of some semi-terrestrial amphipods. *Rept. Dove Mar. Lab.*, 3rd ser., No. 12: 49–62.

Williamson, D. I. 1951b. Studies on the biology of Talitridae (Crustacea, Amphipoda): Effects of atmospheric humidity. *J. Mar. Biol. Assoc.*, U. K., 30(1): 73–90.

Williamson, D. I. 1951c. Ibid: Visual orientation in *Talitrus saltator*. *Ibid:* 91–99.

The Role of European Species in the Newfoundland Fauna of Chilopods, Diplopods and Terrestrial Isopods

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ABSTRACT

Of these groups, altogether 42 species are now known from Newfoundland, the majority (9 Chilopods, 15 Diplopods and 12 Oniscoids) being introduced European forms. It is suggested that the majority of the European forms now often very abundant in Nfld were introduced during the period when sailing vessels carried ballast and when establishment of agriculture and gardening created suitable conditions for such species which in their original area live in ± open localities. The European origin of these species can be argued from following features of their present distribution and ecology: (1) They are in Nfld generally restricted to cities, settlements and their immediate surroundings, (2) they often belong to phylogenetic groups of Old World origin, 3) they occur in Europe in localities where they have great chances of being carried away. Part of the introduced species are now permanently settled in the area of introduction, whilst others are still largely dependent on man and will probably not be able to survive the climate of Nfld out-of-doors.

It is well-known that a number of Old World organisms have been introduced to North America since the time of arrival of the first white colonists, and then become settled in more or less extensive areas of this continent. Striking examples of such cases have been presented by Brown (1940 and 1950), Palmén (1951, 1952 and 1954) and Lindroth (1955 and 1958). The soil-inhabiting Chilopods, Diplopods and Oniscoids are particularly suitable for studies of the consequences of such an introduction.

The features of local distribution and abundance of European species of Chilopods, Diplopods and Oniscoids in Newfoundland was studied by a Finnish-Swedish biological expedition in 1949, and the data obtained were still increased by Dr. C. H. Lindroth during his trip to Newfoundland in 1951. Before this time, only one species of Chilopods, 4 species of Diplopods and 3 species of Oniscoids were known from this island. For the present the numbers are 12, 18 and 12, respectively. In spite of the poorness of the fauna, it gives an interesting example of establishment of originally introduced animals in the area of importation.

It is a striking feature of the Newfoundland fauna of these groups that the number of endemic American species is low, and, moreover, that the abundance of the endemic American species is low in comparison with many of the introduced species. The entire group of terrestrial Isopods consists of European species, the Diplopods are represented by two nearctic species only (*Underwoodia polygama* Cook & Coll., *Trichopetalum ? lunatum* Harger), and the Chilopods by three nearctic species (*Geophilus terrae-novae* Palmén, *Lithobius lindrothi* Palmén, and a still unidentified species of *Lithobius*). Hence of the total of 42 species, only five are nearctic. Of the rest, two species (*Orthomorpha gracilis, Lamyctes fulvicornis*) are cosmopolitian, whilst all other species are of doubtless European origin.

According to the data available, of the endemic American species only *Geophilus terrae-novae* occurs throughout Newfoundland, whilst *Underwoodia polygama* seems to be lacking in the SE, and the three other American species have been found in the western or southwestern parts of the island only. The narrow range of some of these species would hardly seem to be due to any environmental factor, but to the history of immigration. On account of the fact that the active spread of at least many Diplopods and Oniscoides is very slow, repopulation of the glaciated areas of North America after the recession of the ice-sheet by representatives of these groups has proceeded very slowly. It seems probable that species like *Trichopetalum ? lunatum* and *Underwoodia polygama* have not yet been able to colonize the entire area which is within their range or survival, neither have many of the well-known American genera and species of Diplopods and Chilopods that occur in eastern Canada and in the northeastern United States been able to reach Newfoundland which is comparatively isolated geographically.

The bulk of the species of Chilopods, Diplopods and Oniscoids now known from Newfoundland belong to a faunal type rather familiar to the major part of Europe, including Scandinavia and Finland in the north. The European origin of the Newfoundland populations of these species may be argued from certain features of their distribution and ecology, viz.: (1) The present distribution of these species in Newfoundland (and, in many cases, in entire N. America) shows close correlation with the distribution of human settlements, many species being entirely restricted to the settlements and their surroundings. (2) Many of the species in question belong to phylogenetic groups of Old World origin, i.e. genera which have no American representatives (e.g. *Trachelipus*). (3) In the Old World they usually are common and often abundant in such localities where they have great chances of being carried away, e.g. with ballast, as demonstrated very clearly by Lindroth (1956). In many of these species these requirements are fulfilled simultaneously.

Of the Old World species now known from Newfoundland, the following have so far found in or just around human settlements only, thus still indicating their immigration history very clearly:—

Chilopoda

Haplophilus subterraneus (Leach)
Schendyla nemorensis (C. Koch)
Necrophloeophagus longicornis (Leach)
Geophilus electricus L.
Cryptops parisi Brol.
Lithobius forficatus (L.)
L. melanops Newp.
L. microps Mein.

Diplopoda

Brachydesmus superus Latz.
Polydesmus inconstans Latz.
P. denticulatus (C.L.Koch)
Ophiodesmus albonanus Latz.
Nopoiulus venustus (Mein.)
Choneiulus palmatus (Nemec)
Proteroiulus fuscus (am Stein)
Blaniulus guttulatus Bosc.
Cylindroiulus frisius (Verh.)
C. britannicus (Verh.)
C. silvarum (Mein.)
C. truncorum (Silv.)
C. teutonicus (Poc.)
Ophyiulus fallax (Mein.)
Brachyiulus littoralis (Verh.)

Oniscoidea

Trichoniscus pusillus pusillus (Brandt)
T. provisorius Racov.
T. pygmaeus Sars
Trichoniscoides sarsi Pat.
Androniscus dentiger Verh.
Hyloniscus riparius (C.L.Koch)
Haplophthalmus danicus B.–L.
Oniscus asellus L.
Porcellio scaber Latr.
P. dilatatus Brandt
Trachelipus rathkei (Brandt)
Cylisticus convexus (DeG.)

A number of the species listed above have so far been found in such localities only where they may be able to hibernate under man-made conditions. Hence there is no evidence about their being permanently settled out-of-doors in this area. Among the Chilopods *Haplophilus subterraneus*, *Cryptops parisi* and *Lithobius melanops*, among the Diplopods at least *Ophiodesmus albonanus*, *Nopoiulus venustus*, *Choneiulus palmatus* and *Cylindroiulus truncorum* belong to this group, and among the Oniscoids *Trichoniscus pygmaeus*, *Trichoniscoides sarsi*, *Androniscus dentiger*, *Hyloniscus riparius* and *Porcellio dilatatus*. These species are particularly interesting because they still prove their European origin very clearly.

Many of the European species seem to have become permanently settled in Newfoundland. In this respect *Lithobius forficatus* among the Chilopods, and three Oniscoids (*Trichoniscus pusillus pusillus*, *Oniscus asellus* and *Porcellio scaber*) should be especially mentioned; these species have without doubt become native elements of the Newfoundland fauna in spite of their comparatively recent European origin, and they now have a rather wide range in this area. Other species are restricted to rather narrow areas of Newfoundland, but except human settlements they have been able to occupy a number of localities nearby. There are a number of finds of these species from such localities where they without doubt have been able to survive for generations quite independently of man and where they thus have been able to hibernate out-of-doors. Typical examples of species of this type are the Chilopods *Schendyla nemorensis*, *Necrophloeophagus longicornis*, *Lithobius microps* and the cosmopolitian species *Lamyctes fulvicornis*, the Diplopods *Brachydesmus superus*, *Proteroiulus fuscus*, *Blaniulus guttulatus*, *Cylindroiulus silvarum*, *Ophyiulus fallax* and *Brachyiulus littoralis*, and the Oniscoids *Trichoniscus provisorius* and *Cylisticus convexus*. In spite of intensive search, however, none of these species were found further away than some few kms. from the nearest settlement.

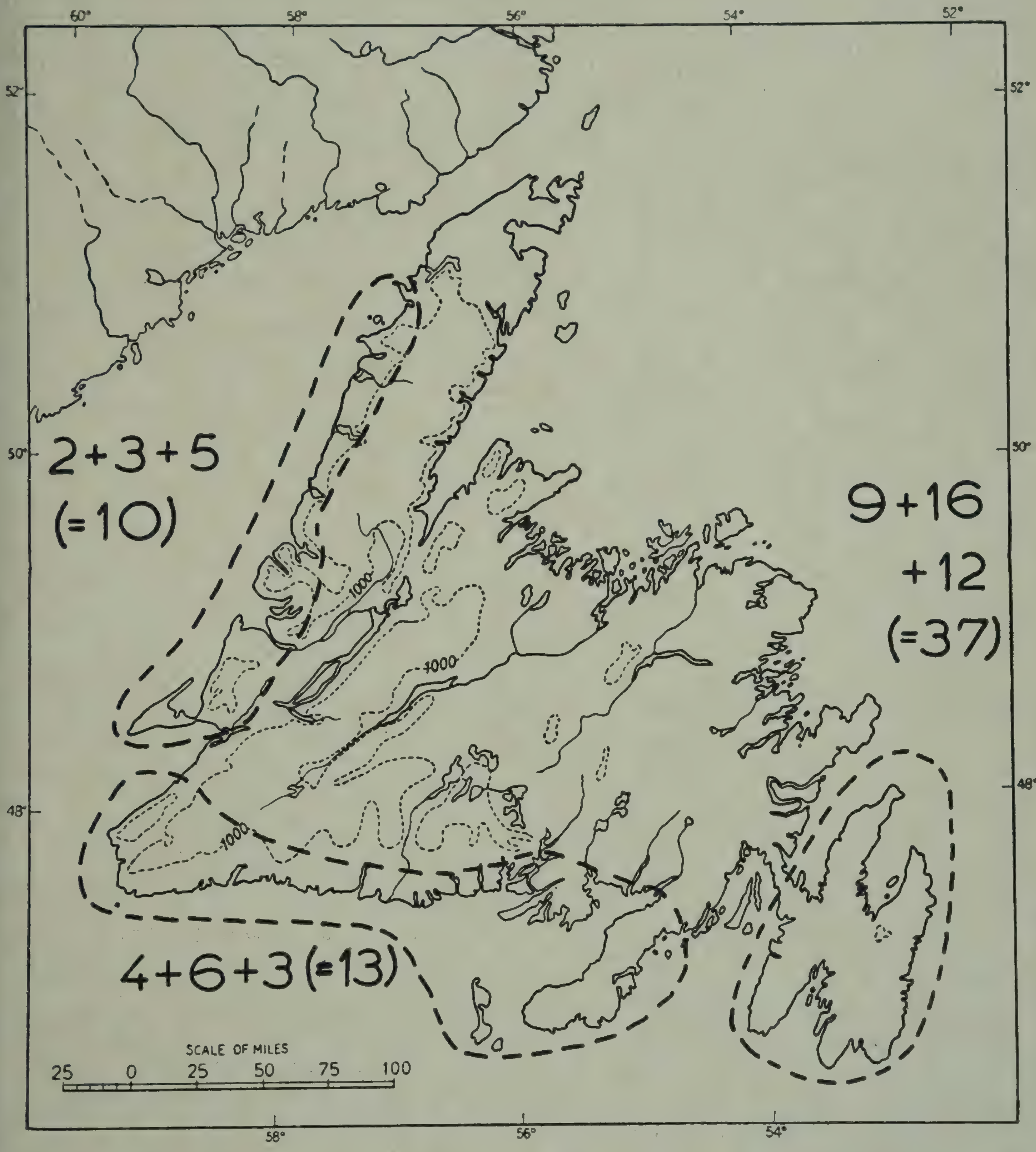

Fig. 1. Numbers of European species of Chilopods, Diplopods and Oniscoids in different costal areas of Newfoundland, according to the survey of 1949 and 1951. Only six out of the 37 European species (*Lithobius forficatus*, *Lamyctes fulvicornis*, *Proteroiulus fuscus*, *Trichoniscus pusillus pusillus*, *Oniscus asellus*, *Porcellio scaber*) are known from areas other than those indicated on the map.

Fig. 1 demonstrates the differences in numbers of the European species of Chilopods, Diplopods and Oniscoids between the southeastern, southern and western coastal areas of Newfoundland. The Avalon Peninsula in the southeast seems to have been the most favoured area for the introduction of Old World organisms. There are a number of species which have been found only in this area, whilst not a single of the European species is absent from the Avalon Peninsula. Species restricted to the Avalon Peninsula are the Chilopods *Haplophilus subterraneus*, *Geophilus electricus*, *Schendyla nemorensis*, *Cryptops parisi* and *Lithobius melanops*, the Diplopods *Polydesmus denticulatus*, *Ophiodesmus albonanus*, *Choneiulus palmatus*, *Nopoiulus venustus*, *Blaniulus guttulatus*, *Cylindroiulus britannicus*, *C. silvarum*, *C. truncorum*, and *C. teutonicus*, and the Oniscoids *Trichoniscus provisorius*, *Trichoniscoides sarsi*, *Androniscus dentiger*, *Hyloniscus riparius* and *Trachelipus rathkei*. The comparatively high number of European species occurring on the Avalon Peninsula would seem to be due to the fact that this area has many well-known landing-places of European colonists of the 16th and 17th century (Placentia, Ferryland, St. John's, e.g.), and moreover, that there has been intensive communication between this area and Europe particularly during the period of sailing-vessels carrying ballast, as demonstrated recently by Lindroth (1958).

For more detailed reference concerning the Newfoundland fauna of Chilopods, Diplopods and Oniscoids, three previous papers of the present author (Palmén 1951, 1952 and 1954) should be consulted.

REFERENCES

Brown, W. J. 1940. Notes on the American distribution of some species of Coleoptera common to the European and North American continents. *Can. Entomol.* 72: 65–78.

Brown, W. J. 1950. The extralimital distribution of some species of Coleoptera. *Can. Entomol.* 82: 197–205.

Lindroth, Carl H. 1955. The carabid beetles of Newfoundland, including the French islands St. Pierre and Miquelon. *Opusc. Entom., Suppl.* 12: 1–160.

Lindroth, Carl H. 1958. The dispersal of insects by human agencies across the North Atlantic. *Proc. 10th Int. Congr. Ent.*, Montreal. (Abstract, in press).

Palmén, Ernst. 1951. A survey of the Oniscoidea (Isopoda terr.) of Newfoundland. *Ann. Zool. Soc. Zool. Bot. Fenn. "Vanamo"* 14(1): 1–27.

Palmén, Ernst. 1952. Survey of the Diplopoda of Newfoundland. *Ann. Zool. Soc. Zool. Bot. Fenn. "Vanamo"* 15(1): 1–31.

Palmén, Ernst. 1954. Survey of the Chilopoda of Newfoundland. *Arch. Soc. Zool. Bot. Fenn. "Vanamo"* 8: 131–149.

DISCUSSION

M. S. Ghilarov. Do you suggest that the European species of the groups discussed above were taken to Newfoundland in association with shipping or is it possible that they might have been dispersed by means of floating wood, timbers or logs?

Ernst Palmén. So far there is no evidence of such dispersal, at least not in the groups treated in this connection. Since it is necessary to postulate spread with ballast, e.g., at least in all those species that are still entirely restricted to human settlements, the same would seem to be true of all other European species also, particularly because they are often common in such localities where ballast was taken on board the sailing-vessels.

M. S. Ghilarov. Is the part of Canada adjacent to Newfoundland poor in the number of species under discussion?

Ernst Palmén. Yes. The coastal area of NE North America is, however, still insufficiently known in this respect.

M. S. Ghilarov. How do you explain the small populations and small numbers of American species and the predominance of European forms in Newfoundland?

Ernst Palmén. The low number of American species is in my opinion due to slow spread of native American species. On the other hand, all endemic American species except *Geophilus terrae-novae* are woodland species which probably never are particularly abundant, whilst many of the European immigrants are extremely well adapted to open localities (*Porcellio*, *Lithobius forficatus*, e.g.). At least in the case of Oniscoids, the high abundance of certain species might to a certain degree be due to the high humidity of the air along the coasts of Newfoundland.

M. S. Ghilarov. What is the distributions of European species in North America?

Ernst Palmén. A few species have spread across the continent (*Lithobius forficatus*, *Porcellio scaber*, e.g.), but they still show a clear correlation with the distribution of human settlements in many areas of the American mainland. A high number of the European immigrants is, however, restricted to the Atlantic and/or Pacific coasts where there are large harbours.

The Palpal "Tined Seta" in the Mesostigmata, a Homologue of the Palpal Claw in the Onychopalpida (Acarina)

By Joseph H. Camin[1], Gordon M. Clark[2], and Flora Gorirossi Bourdeau[3]

While examining a series of mites by means of polarized light during the summer of 1954 at the University of Maryland's Institute of Acarology, it was observed that the claws of mites in the suborder Mesostigmata exhibit birefringence. It was further noted that, although none of the other setae of the body or appendages exhibit this phenomenon, the so-called "tined setae" of the palpal tarsi are also birefringent. This suggested that the tined "setae" might not be setae at all, but remnants of palpal tarsal claws, homologous with those present in the suborder Onychopalpida. Examination of several species of onychopalpid mites by means of polarized light revealed that in these also, the claws of the legs and palpi are birefringent, but the setae are not. Zakhvatkin (1952) has placed considerable taxonomic importance on the phenomenon of birefrigence or the presence or absence of actinochitin in the various groups of Acarina and other chelicerate arthropods. Grandjean (1954) also suggested the probable homology of the mesostigmatid palpal "tined setae" and the onychopalpid palpal claws on the basis of the negative birefringence exhibited by these structures.

A review of the onychopalpid families Opilioacaridae With, 1902, and Holothyridae Thorell, 1882, revealed that there is considerable variation in the palpal claws. All of the described species of Opilioacaridae possess a pair of typical ambulacral claws at the tip of each palpal tarsus (Fig. 1). In some of these, the claws are comparatively well-developed and are almost as large as those of the legs. In others they are greatly reduced. The palpal tarsi of at least one form, an undescribed species collected by Ted Tibbetts[4] in Puerto Rico, are highly modified (Fig. 2). The tip of the tarsal segment is attenuated and a very robust claw, possessing several projections, appears to have migrated medially and toward the proximal end of the tarsus. In both structure and position, it remotely resembles the "tined seta" of the palpal tarsus in the Mesostigmata.

The more primitive Holothyridae also possess a pair of relatively unmodified ambulacral claws on each palpal tarsus, but these are not located at the tip. On the most primitive form examined, *Holothyrus constrictus* Domrow, the claws are strong, bifid and located near the tip, but on the mesial aspect of the tarsus (Fig. 3). Two distinct claws are also present, closer to the proximal end of the tarsus, on the palp of *H. australasiae* Womersley (1935). The more distal one is well-developed and distinctly claw-like. The other is bifid and more closely resembles the "tined seta" of the Mesostigmata than a typical claw (Fig. 4). In other species, such as *H. coccinella* Gervais, a well-developed claw is present near the base of the palpal tarsus (Fig. 5). This claw has two or more tines and it is uncertain whether it represents a single claw or the fusion of two claws, perhaps including the pretarsal armature to which the claws attach.

The so-called "tined setae" at the bases of the palpal tarsi of the mesostigmatid mites are much more robust and claw-like in the large, predaceous species (Fig. 6) and even in the semi-parasitic forms (Fig. 7) than they are in the obligatory parasites (Fig. 8). In the latter, these structures are often greatly reduced and, indeed, more closely resemble setae than claws. It is in the descriptions of these parasitic mites that this organ became known as the "tined seta" or "specialized sensory seta" of the palpal tarsus.

The foregoing data suggest that there has been a general tendency toward the migration of the palpal claws from the tip of the palpal tarsus to the base in the Onychopalpida, with the accompanying reduction and loss of one claw of each pair or the fusion of the two claws. It is further suggested that reduction of the remaining claw or the fused claws has continued from the predaceous Mesostigmata to their parasitic relatives. All of this, however, is merely circumstantial evidence and cannot be construed as proof of the true nature of the mesostigmatid "tined seta".

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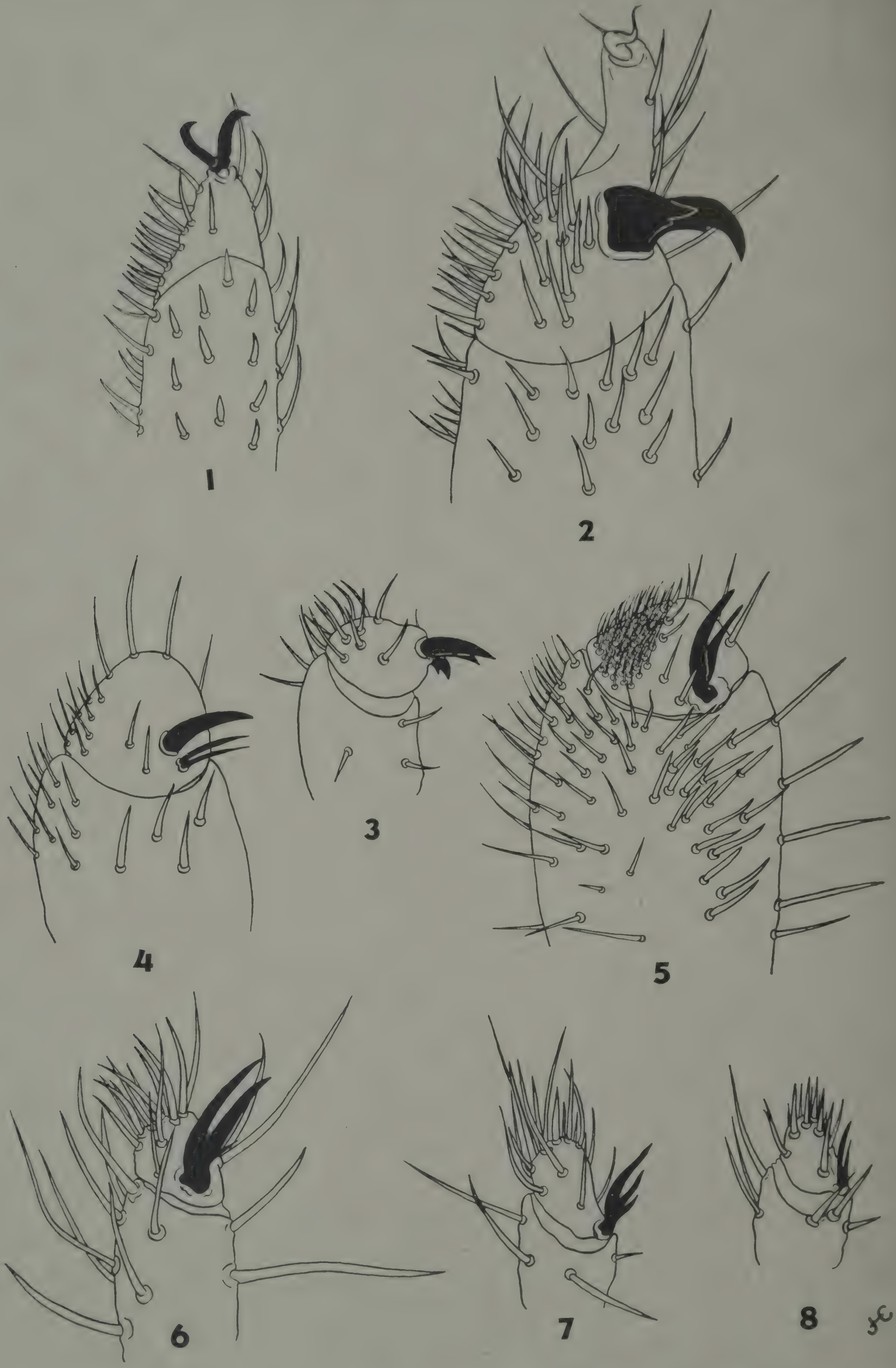


Figs. 1–8. Palpal tibiae and tarsi of onychopalpid and mesostigmatid mites, showing palpal claws and "tined setae": 1. *Opilioacarus* sp.; 2. Opilioacaridae, undescribed; 3. *Holothyrus constrictus* Domrow, 1955; 4. *Holothyrus australasiae* Womersley, 1935 (after Womersley); 5. *Holothyrus coccinella* Gervais, 1842; 6. *Megisthanus floridanus* Banks, 1904; 7. *Macrocheles muscae-domesticae* (Scopoli, 1772); 8. *Ophionyssus natricis* (Gervais, 1844).

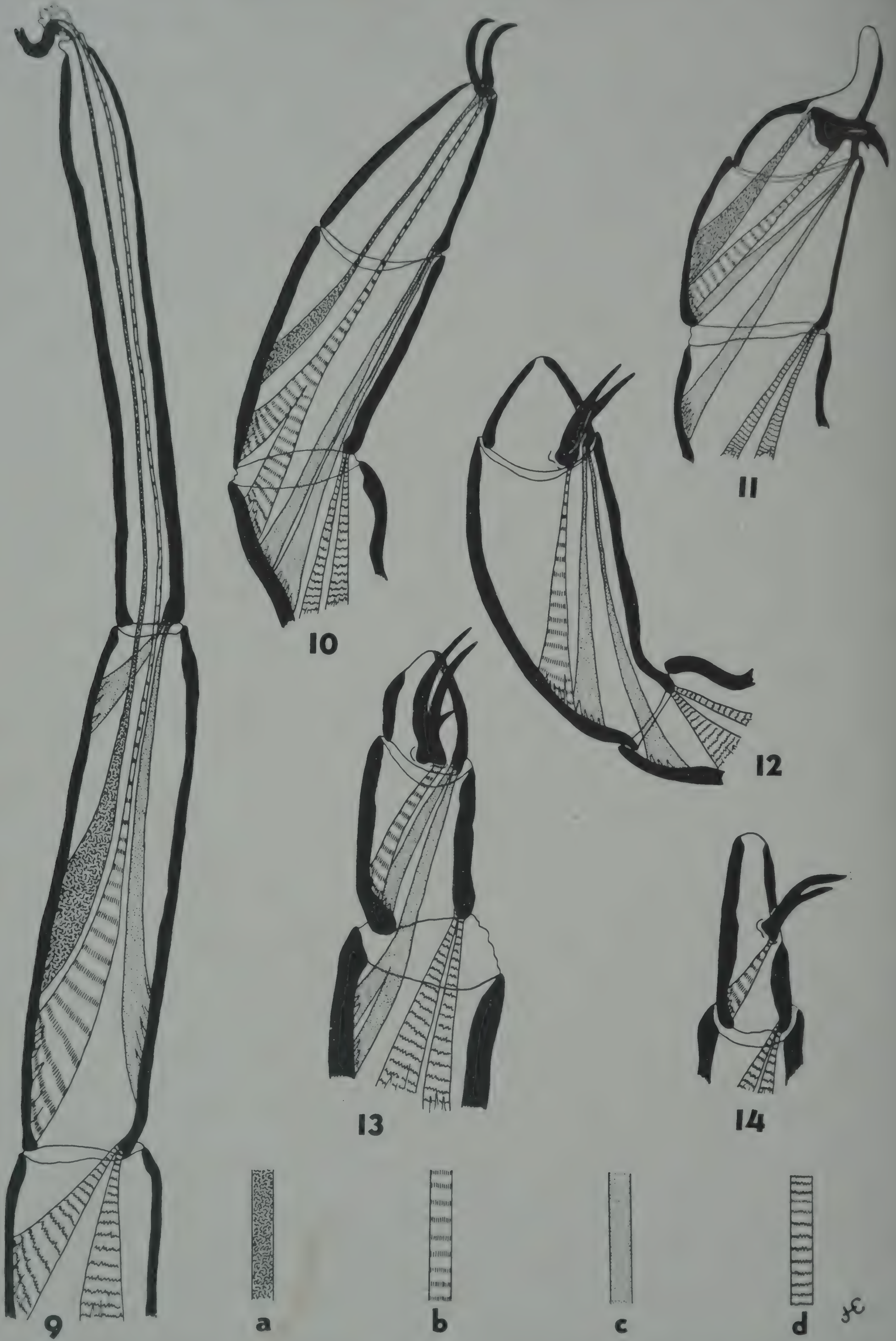
In order to determine whether or not the "tined setae" of the Mesostigmata are actually homologous with the palpal claws of the Onychopalpida, it was necessary to investigate the musculature of the palps in these two groups of mites, to compare the palpal musculature of the Mesostigmata and the Onychopalpida, and to compare the palpal musculature with that of the legs.

In *Opilioacarus*, the most primitive described genus in the suborder Onychopalpida, three sets of muscles are concerned in the operation of the tarsus and pretarsus of the leg (Fig. 9). These are the elevator and depressor of the pretarsus and a pair of tarsal flexors. The segments distal to the trochanter, in almost all of the Acarina examined in this study, are equipped only with flexor muscles. Extension of the appendages appears to be accomplished by means of hydrostatic pressure, which is supplied by the contraction of several body muscles. These compress the mite dorsoventrally, forcing body fluids into the hollow appendages. The flexor muscles oppose this hydrostatic pressure instead of antagonistic extensor muscles.

The pretarsal elevator muscle in the leg of *Opilioacarus* inserts on a sclerotized central armature, to which the claws are attached by ligaments, and has its origin in the tibia. Contraction of this muscle draws the claws together and elevates the entire pretarsus. The depressor of the pretarsus inserts by means of a divided tendon directly on the bases of the two claws and also arises in the tibia. Contraction of the depressor spreads the claws and depresses them and the entire pretarsus, enabling the mite to grasp the substrate. The pair of tarsal flexors insert ventrally at the proximal end of the tarsus and have their origins in the tibia. The leg musculature in other onychopalpids and in the mesostigmatid mites is quite similar to that of *Opilioacarus*, but with a few modifications. In some species, one or both of the tarsal flexors may originate in the next proximal segment, the genu, rather than in the tibia. In most related species of Onychopalpida and Mesostigmata, the tibia and tarsus have fused and the tarsal flexors have been lost. The pretarsal elevator muscles in the legs of the Holothyridae and the Mesostigmata are much like those of the Opilioacaridae, except that in some forms the muscle is partly divided at its origin and has a small part of the muscle band arising in the genu. The entire pretarsus is often somewhat modified in most of the more highly evolved groups. The base of the pretarsus is hollow and conelike in some. In these mites the contraction of the pretarsal elevator muscle retracts the central armature and the claws into the cone, bringing the claws together and folding the fan-like caruncle between them, and then raises the entire pretarsus. The depressor of the pretarsus, while depressing the pretarsus and claws, spreads the claws and extrudes them from the pretarsal base and also spreads the caruncle. This muscle is often divided at its origin, with one part arising in the genu and the other in the tibia. In most of the Mesostigmata the pretarsal depressor has a single origin which has shifted entirely into the genu.

Because of the modifications that have arisen with the fusion of segments and the apparent shifting of joints in some of the more highly evolved forms, it is often difficult to homologize the palpal musculature and segmentation with that of the legs. However, the palpal musculature of the mesostigmatid and holothyrid mites is readily comparable with that of the palps and of the legs of the Opilioacaridae.

The musculatures of the leg and palp of *Opilioacarus* are very similar, except that with the foreshortening of the palpal segments there appears to have been some shifting of muscle origins or of the joint between the tibia and genu. The pretarsus and the pretarsal elevator of the palp are almost exactly like those of the leg. The pretarsal depressor is easily recognized, but has a divided origin with part of the muscle band arising in the genu (Fig. 10). Both tarsal flexors of the palp arise in the genu rather than in the tibia, as they do in the leg. In the palp of the undescribed Puerto Rican species of opilioacarid, mentioned previously, both pretarsal muscles and the pair of tarsal flexors are present as in other more typical Opilioacaridae. However, in this species, both the elevator and the depressor of the pretarsus insert directly on the base of the very strong single claw, thus indicating that this structure actually represents a fusion of all of the sclerotized elements of the pretarsus—the two claws plus the central armature to which these ordinarily attach (Fig. 11). Each of these muscles has only a single origin in the tibia. Both of the tarsal flexors insert ventrally on the proximal margin of the tarsus, as they do in the palps and legs of other opilioacarid species, but one arises in the tibia, the other in the genu. This arrange-



Figs. 9–14. Musculature of leg and palpal tibiae, tarsi and pretarsi of onychopalpid and mesostigmatid mites: 9. Leg of *Opilioacarus* sp.; 10. Palp of *Opilioacarus* sp.; 11. Palp of undescribed Opilioacaridae; 12. Palp of *Holothyrus coccinella* Gervais, 1842; 13. Palp of *Megisthanus floridanus* Banks, 1904; 14. Palp of *Echinomegistus wheeleri* (Wasmann, 1902). a. pretarsal elevator muscle; b. pretarsal depressor muscle; c. tarsal flexor muscle; d. tibial flexor muscle.

ment is similar to that found in the legs of more highly evolved onychopalpid and mesostigmatid mites.

The muscle patterns in the palps of *Holothyrus coccinella* (Fig. 12), an onychopalpid, and of mesostigmatid mites, such as *Megisthanus floridanus* Banks (Fig. 13), are exactly like that of the Puerto Rican opilioacarid, except for the loss of the pretarsal elevator muscle. The claw in the one case and the "tined seta" in the other are each set in an elastic membrane. The membrane tends to keep the structure appressed to the tarsal segment. The depressor muscle opposes the action of the membrane and pulls the claw or "seta" into a position at right angles to the palp. Thus, when the depressor muscles are contracted, the claws or "setae" of the two palps oppose each other and perhaps function as grasping organs in the handling of food.

The minute size of such a structure as the palp of a mite sometimes makes it difficult to be certain of the attachments of its muscles. At first, using cleared whole mounts of the palps, it appeared that the depressor of the "tined seta" might not insert on the base of the "seta" at all, but on the base of the tarsal segment, thus making it merely a third band of tarsal flexor muscle. However, serial sections of several palps from different mite species clarified the matter and showed unmistakably that this muscle inserts on the "seta" and is, therefore, the homologue of the pretarsal depressor muscle of the onychopalpid mites. This was further elucidated by a study of the palpal musculature of *Echinomegistus wheeleri* (Wasmann), a member of the mesostigmatid family Paramegistidae (Fig. 14). In all members of this family the palpal tibiae and tarsi are fused with each other to form a single functioning segment and there is the accompanying complete loss of tarsal flexor muscles. The "tined seta" is well-developed in these predaceous mites and it can be readily observed that a strong muscle, the pretarsal depressor, arises in the tibial portion of the distal segment of the palp and inserts on the base of the "tined seta".

The fact that none of the true setae of the body or appendages of either the onychopalpid or mesostigmatid mites are activated by muscles indicates that the "tined setae" of the mesostigmatid palpal tarsi, which are so activated, are not true setae. The musculatures of the palps of *Opilioacarus*, *Holothyrus* and the Mesostigmata, especially the latter two (Figs. 12 and 13), are so similar that it is unreasonable to interpret them as anything but homologous. Therefore, it has been clearly demonstrated that the so-called "tined seta" of the mesostigmatid palpal tarsus is actually a claw and is a homologue of the palpal claw of the Onychopalpida.

Proof of the true nature of the palpal claw of the Mesostigmata was obtained quite by accident. Several snake mites, *Ophionyssus natricis* (Gervais), were macerated in saline in order to observe protozoan sporozoites, of which these mites are vectors. When these macerated mites were observed through the microscope, it was noted that although the legs were not moving, the claws and pretarsi of the legs were being depressed and elevated spasmodically. At the same time, although the palps were immobile, the palpal claws were also twitching due to the spasmodic contraction of the pretarsal depressor muscle, which was readily observed with the phase contrast microscope.

The suborder Onychopalpida Wharton, 1947, (Baker and Wharton, 1952), was erected largely because of the palpal claws that these primitive mites possess. With the discovery that the Mesostigmata also have palpal claws, the question arises as to the validity of the separation of the two suborders. A study of the two groups of mites reveals that there are sufficient differences remaining to distinguish the two suborders, even though they can no longer be separated on the basis of the presence or absence of palpal claws.

The onychopalpids are, in general, much more primitive than the mesostigmatid mites. In the Onychopalpida, the palpal coxae are only partially fused ventrally and are not fused dorsally at all, so that the chelicerae are free and uncovered. The palpal coxae of all Mesostigmata, including more than sixty families of mites, are fused both ventrally and dorsally to form a tube through which the movable mouthparts are guided. Dorsally a tectum covers the chelicerae.

Universally among the Mesostigmata there are three pairs of hypostomal setae and a single pair of gnathosomal setae placed ventrally on the gnathosoma. There are no dorsal gnathosomal setae, except for those on the palps. The Onychopalpida possess numerous hypostomal and gnathosomal setae, ventrally and dorsally.

The tritosternum in the Mesostigmata consists of a fused base from which a pair of lacinae arise. The lacinae are usually partly fused at their proximal ends and in some cases they are fused for their entire length. When the tritosternum is present in onychopalpid mites, it consists of two completely independent structures, each with its base and single lacina arising out of the base.

Three pairs of lyriform sternal pores are usually present in the mites of both suborders. Associated with these pores there are almost always four primary pairs of sternal setae in the Mesostigmata. Many assymetrically placed sternal setae are present in the Onychopalpida.

Among other characters that serve to distinguish the Onychopalpida from the Mesostigmata are the number and structure of the lateral stigmata. Except for a few endoparasitic forms, the stigmata are placed lateroventrally in the Mesostigmata. These mites possess a single pair of stigmata that are usually located between the third and fourth coxae. In some of the more highly evolved uropodine mites the stigmata are opposite coxae III or between coxae II and III. Arising from the stigmata and extending anteriorly in all Mesostigmata, excepting some of the endoparasites, are a pair of tubular peritremes. Two to four ventral or dorsal stigmata, lacking peritremes, are present in the Onychopalpida. In *Holothyrus*, there is one pair of ventro-lateral stigmata between coxae III and IV, as in the Mesostigmata, and a second pair is located just behind coxae IV, as in the ticks. There is much suggestive evidence that the holothyrid Onychopalpida may represent a primitive offshoot of an original stock that perhaps gave rise to both the suborder Mesostigmata and the suborder Ixodides, but that interesting problem needs further investigation.

REFERENCES

Baker, E. W., and G. W. Wharton. 1952. An introduction to acarology. p. 36. *Macmillan Co.*, New York.

Grandjean, Francois. 1954. Sur les nombres d'articles aux appendices des Acariens actinochitineux. *Arch. des Sciences*, Geneva 7(5): 335–362.

Womersley, H. 1935. A species of Acarina of the genus *Holothyrus* from Australia and New Zealand. *Ann. Mag. Nat. Hist.* (10), 16: 154–157.

Zakhvatkin, A. A. 1952. Introduction to the systematics of the Acari in relation to the Chelicerata. *Mag. Parasit.*, Moscow 14: 5–46. (In Russian).

Host Specificity of Bird Nasal Mites (Rhinonyssidae) is a Function of the Gregariousness of the Host

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ABSTRACT

If birds are non-gregarious, e.g. owls (Strigiformes), each species will have a species of nasal mite visibly distinct from that of another species of host; if the birds are gregarious interspecifically, e.g. ducks and geese (Anseriformes), and the Icteridae (Passeriformes) all the host species will have a morphologically similar species of nasal mite.

This holds true only so long as the birds are closely related; for example, it is not unusual for grebes (Colymbiformes) to be associated with ducks, but they will not be parasitized by the duck mites, or vice versa.

It is, of course, the usual thing for internal parasites to show some degree of host specificity. How pronounced this specificity may be depends upon many factors. Here we want to explore briefly only the apparent effect of isolation or gregariousness of the host birds on degree of specificity of nasal mites.

Nearly all genera of bird nasal mites are restricted to related groups of birds: for example *Rhinoecius* is found only in Strigiforme birds; *Paraneonyssus* and *Ptilonyssus* are found only in Passeriforme birds; *Neonyssus* only in Ciconiiforme and Columbiforme birds, etc. The nasal mite genus *Sternostoma* is a notable exception to this rule, but it holds well for all others.

If we assume that nasal mites began to parasitize birds at about the time that the major bird orders were evolving, and that these emergent orders did not mingle with each other, then we can see that a restriction to free gene exchange would occur and that various mite types would stabilize along with their hosts.

Now if within each of the larger bird groups individual species isolate themselves from other species of the genus, then the mites they harbor would experience further restricted gene exchange and such mites would tend to stabilize as distinct species. If on the other hand several species, or even genera, of related birds continually mingle with each other, then the mites they harbor should tend to remain homogeneous.

What is the evidence favoring such an hypothesis? The Anseriforme birds; ducks, geese, swans, and mergansers are highly gregarious. A single pond, or lake, or grain field, may contain many kinds of Anseriformes in close association with each other. If the hypothesis is to hold, then certainly all Anseriformes should have a common species of nasal mite. Records from North America, Europe, Asia, and Africa, and from 10 species of duck, 4 species of geese, 2 species of swans, and 2 species of mergansers bear out the truth of the hypothesis. All have the same nasal mite species, *Rhinonyssus rhinolethrum* (Trouessart). There are some slight differences in those from some hosts, but they are slight indeed.

The tree ducks and the flamingos are notable examples of Anserids that do not mingle with others of the order and it will be most interesting to investigate their mites. They should show greater variation from *Rhinonyssus rhinolethrum* than exists in known forms.

Other birds with highly gregarious tendencies during at least part of every year are the herons and egrets, the Ciconiiformes. They may be quite isolationist during feeding activities but nesting colonies may contain many species in close association. Thus far we have only 4 records from 3 species of herons. These have been described as two species but they are very nearly identical and I feel convinced they represent only one species, *Neonyssus belepolskyii* Bregetova, 1950. (Syn., *N. ardeae* Zumpt and Till, 1955). It must be noted here that a third species of mite, *N. bubulci* Zumpt and Till, 1955, has been described from the cattle egret, *Bubulcus ibis*. This egret tends to remain aloof from other Ciconiids and it is not surprising that the mite it harbors shows noticeable differences.

The small charadriiforme shore birds, the plovers, snipes, and sanderlings, are quite gregarious, and under condition which would favor successful mite transfer; a highly humid substrate. Four species of *Rhinonyssus* have been described from 8 species of small shore birds but these are all referable to one species, *Rhinonyssus coniventris* Trouessart.

It will be most interesting to note the mites of the killdeer, *Charadrius vociferus*, a strictly upland plover which does not associate with other plovers. Examination of about 10 birds has thus far failed to reveal any nasal mites.

We do know that one individualistic wader, the black-necked stilt, *Himantopus mexicanus*, has a species of *Rhinonyssus* different from that of other shore birds.

Other charadriiforme birds, mingling rather freely with the small waders, but quite different in habits are the gulls and terns—family Laridae. They are gregarious interspecifically and harbor the same mite, *Larinyssus orbicularis* Strandtmann, 1948. This is based on records from 3 continents and 6 species of larids.

The largest and most specialized bird order, Passeriformes, has many gregarious and non-gregarious species. Perhaps the most notoriously gregarious, at least in North America, are the blackbirds, family Icteridae. Many different species of these birds collect in large flocks every fall and are in very close association all winter. Mites from 8 species of blackbirds and orioles proved to be the same species, *Pareneonyssus icteridium* Strandtmann and Furman, 1956.

On the other hand, if the birds are highly individualistic and do not mingle with related species, then by the mechanism of isolation, their nasal parasites should have become distinct from the nasal mites of related birds. However, if our basic assumption is true, that birds became parasitized about the time the modern orders began to emerge, then the nasal mites of birds within an order should be more closely related to each other than to mites of birds of other orders.

In the owls, order Strigiformes, we find the best supporting evidence for our thesis. Owls are non-gregarious and also have a high parasitemia rate. Records from seven species of owls collected in North America, Thailand, Europe, and Africa, show that each species has a distinct parasite species. But, as is to be expected, the mites are closely related and congeneric. The owls and their mites are: from Belgium, *Asio otus,—Rhinoecius otis* Cooreman, 1946; from Africa, *Asio capensis,—Rhinoecius africanus* (Zumpt and Till, 1951); from North America, *Speotyto cunicularia,—Rhinoecius bisetosus* Strandtmann, 1952; *Strix varia,—Rhinoecius cooremani* Strandtmann, 1952; *Bubo virginiana,—Rhinoecius grandis* Strandtmann, 1952; from Thailand, small forest burrowing owl,—*Rhinoecius*. n. sp.

Very incomplete records from the Columbiformes (the pigeons and doves) indicate that isolation has produced distinct species here also. Intraspecifically, columbiforme birds are very gregarious, but not interspecifically. From many parts of the world the common rock pigeon, *Columba livia*, is known to harbor the mite *Neonyssus melloi* Castro, 1948. The common wild American dove, *Zenaidura macroura*, harbors a quite distinct but obviously related mite, *Neonyssus zenaidurae* Crossley, 1952. Unfortunately, no other species of Columbiformes have been investigated. It is interesting to note that Crossley (1950) in a study of North America (Texas) *Columba livia* found a second species of nasal mite, *Neonyssus columbae*, which shows more likeness to *Neonyssus melloi* than to *Neonyssus zenaidurae*. This could mean that continental isolation has produced a new species or it could mean that the rock pigeon has 2 species of *Neonyssus*, but that the second species has just not been found elsewhere. The two species were never found in the same host.

An interesting phenomenon is manifest in the Colymbiforme birds (grebes). These birds do not mingle with other species of Colymbiformes but they frequently are in very close association with large flocks of coots, *Fulica* (Ralliformes), or of ducks (Anseriformes), yet they do not harbor the same mite as either of those birds. Present records, based on only 2 species of grebes, indicate that each grebe species will have a distinct mite species. From the North American eared grebe, *Colymbus caspicus*, we have *Rhinonyssus alberti* Strandtmann, 1956; and from the African *Poliocephalus ruficollis* we have *Rhinonyssus poliocephali* Fain, 1956.

It seems apparent then, that nasal mites have become so adapted physiologically, to their hosts that transfer to distantly related birds will not be successful.

In the Passeriforme birds, those species that do not congregate in close, large, interspecific flocks have their own distinct species of mite. Of several species of grosbeaks, warblers, and vireos thus far examined, each species has a distinct mite. It is true that these birds do form loose interspecific aggregations during migration, but this association is not close enough to allow for mite exchange under the relatively xeric condition in which such birds live.

Admittedly, evidence accrued to date is meager but it seems to indicate that birds which habitually form interspecific congregations will share the same mite species whereas those that live individualistically, or flock only as intraspecific groups, will each have a distinctive nasal mite.

REFERENCES

Bregetova, N. G. 1950. New species of endoparasitic mites of the family Rhinonyssidae. *Reports of the Academy of Science U.S.S.R.* 71: 1005–1008.

De Castro, M. P. 1948. Reestruturação genérica da familia "Rhinonyssidae Vitsthum, 1935" (Acari Mesostigmata: Gamasides) e descrição de algumas especies novas. *Arquivos do Instituto Biologico* 128: 253–284.

Crossley, D. A., Jr. 1950. A new species of nasal mite, *Neonyssus* (*Neonyssus*) *columbae*, from the pigeon. *Proc. Ent. Soc. Washington* 52: 309–312.

Crossley, D. A., Jr. 1952. Two new nasal mites from columbiform birds. *J. Parasitology* 38: 385–390.

Fain, A. 1956. Les Acariens de la famille Rhinonyssidae Vitsthum 1935 parasites des fosses nasales des oiseaux au Ruanda-Urundi. *Rev. Zool. Bot. Afr.* 53: 131–157.

Strandtmann, R. W. 1948. The mesostigmatic nasal mites of birds, I. Two new genera from shore and marsh birds. *J. Parasitology* 34: 505–514.

Strandtmann, R. W. 1952. The mesostigmatic nasal mites of birds, III. New species of *Rhinoecius* from owls. *Proc. Ent. Soc. Washington* 54: 205–214.

Strandtmann, R. W. 1956. The mesostigmatic nasal mites of birds, IV. The species and hosts of the genus *Rhinonyssus*. *Proc. Ent. Soc. Washington* 58: 129–142.

Strandtmann, R. W., and Deane P. Furman. 1956. A new species of mite, *Paraneonyssus icteridius*, from the nasal cavities of blackbirds. *Pan-Pacific Ent.* 32: 167–173.

Zumpt, F., and W. M. Till. 1955. Nasal mites of birds hitherto known from the Ethiopian Region. *J. Ent. S. Africa* 18: 60–92.

A Revision of the Family Nanhermanniidae (Acari: Oribatei)[1]

By Tyler A. Woolley[2] and Harold G. Higgins[3]

ABSTRACT

Prior to this article the family Nanhermanniidae comprised a single genus with five species. In the current revision the genus Masthermannia *Berlese is transferred to the family Nanhermanniidae from the family Hermanniidae. A single species,* Masthermannia mammillaris *Berlese, 1913, is the representative of the genus. This species is differentiated by T-shaped setae inserted in swollen tubercles. Two species of* Posthermannia *Grandjean are included,* P. hirsuta *(Hartman) 1949 and* P. nematomorpha *Grandjean, 1953. These species also possess T-shaped setae, but with longer tenuous arms than those of* Masthermannia. *Six species of* Nanhermannia *Berlese are differentiated by means of a propodosomal T-area, modified T-shaped setae and posterior propodosomal apophyses:* N. nana *(Nic., 1855), Berlese, 1913;* N. elegantula *Berlese, 1913;* N. comitalis *Berlese, 1916;* N. areolata *Strenske, 1953;* N. pectinata *Strenske, 1953; and* N. komáreki *Kunst, 1956. Ecological data and three species of indeterminate position are discussed. A key to the genera and species is also included.*

The principal characteristic of the family Nanhermanniidae Sellnick, 1924, is a crescentic ventral suture between the propodosoma and the hysterosoma. All species of *Nanhermannia* possess this feature. Grandjean (1954) demonstrates this suture in his figures of *Posthermannia nematomorpha*. The characteristic is not mentioned nor figured for *Nanhermannia hirsuta* Hartman, 1949, but Dr. E. W. Baker examined the type specimen for the writers and found the "crescentic suture ventrally semi-surrounding the genital opening." The writers attempted by correspondence to confirm the presence of this suture in *Masthermannia mammillaris* Berlese, 1913, but because of the thickness of the slide on which the type specimen was mounted Drs. Pegazanno and Lombardini found "nothing of particular can be seen of the ventral surface." In spite of this difficulty the authors are of the opinion that there are other structural similarities between these genera which constitute a familial relationship.

The genera *Masthermannia* and *Nanhermannia* were erected as designations for cryptostigmatic mites by Berlese (1913). The type species of the former genus, *M. mammillaris* Berlese, 1913 (= *Angelia mammillaris* Berlese, 1904), possessed T-shaped setae inserted in prominent tubercles (Fig. 2A). Several species of *Nanhermannia* were described by the same author (1913, 1916) with simple setae and simple setal insertions on both propodosoma and hysterosoma. Strenske (1953) shows each seta for these and other species with a minute basal spur (Fig. 2C).

In 1949 Hartman described *Nanhermannia hirsuta* as a new species from Texas, which had prominent T-shaped setae on both propodosoma and hysterosoma. Grandjean (1954) defined a new genus and species, *Posthermannia nematomorpha*, which exhibited T-shaped setae inserted in raised tubercles (Fig. 2B). He placed this species in Nanhermanniidae, compared it to examples of *Nanhermannia* and discussed its relationships with *Masthermannia*. This author had previously (1953) suggested a phylogenetic relationship between *Nanhermannia* and *Masthermannia* on the basis of nymphal characteristics.

As described by their respective authors *Masthermannia* and *Posthermannia* possess swollen dorsal tubercles in which T-shaped setae insert. These tubercles are lacking in Hartman's figure of *N. hirsuta*, but are present in the type, according to Dr. Baker, and the setae are like those of *P. nematomorpha*. The setae of *Masthermannia* are T-shaped, but differ from those of *P. nematomorpha* and *N. hirsuta* in shorter, subequal, less tenuous arms (Figs. 2A, 2B).

All of the species of the genus *Nanhermannia* as herein described possess simple bristles at the base of which is a small spur. The spur, as indicated by Strenske (1953), arises from the same setal insertion as the main bristle, but appears to be fused with the origin of the bristle (Fig. 2C). The writers are of the opinion that the short setal spur of *Nanhermannia* represents a reduction and specialization of one arm of a T-shaped seta. They conclude that all of these types of T-shaped setae (Figs. 2A, B, C) constitute generic

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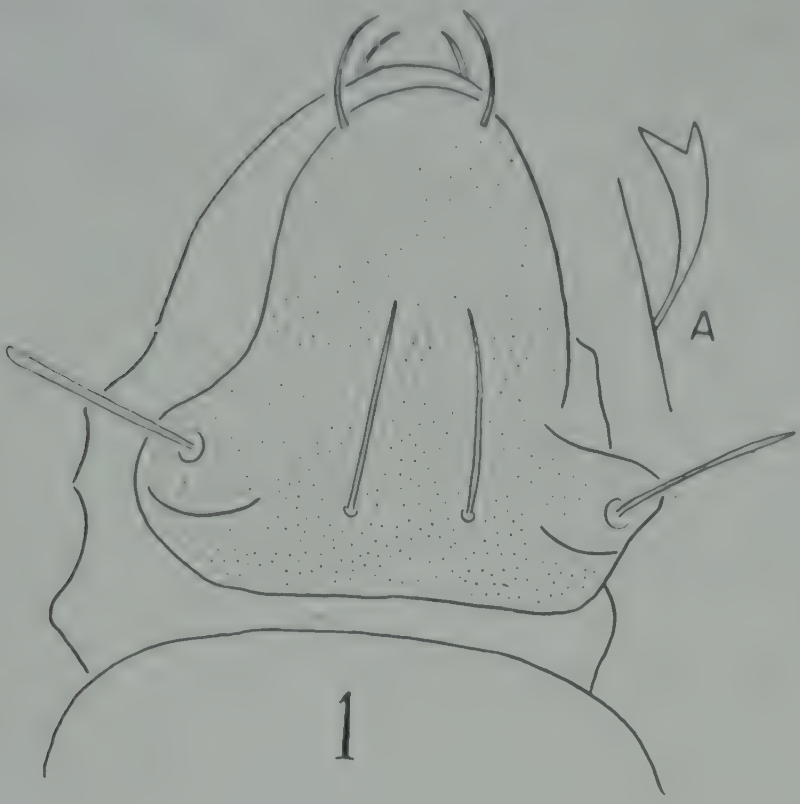

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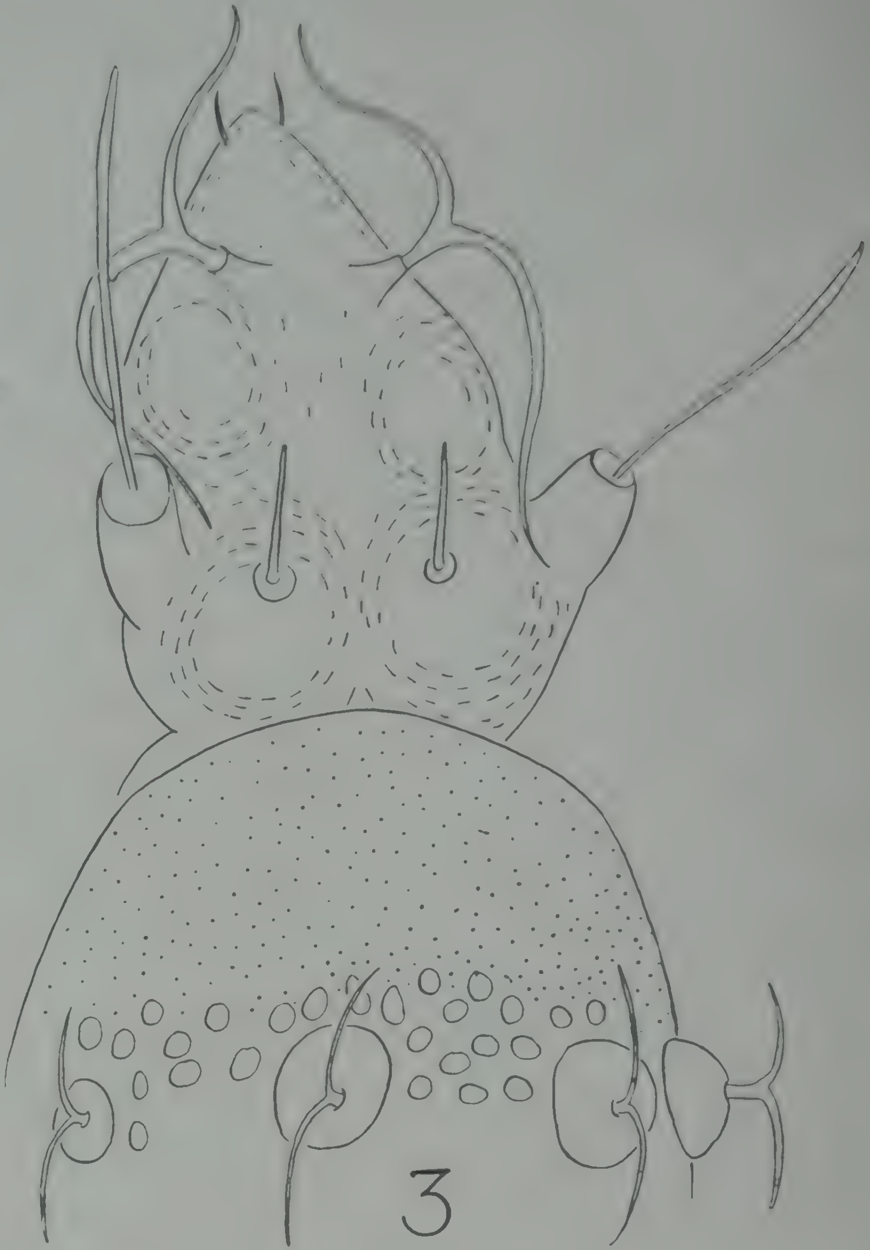

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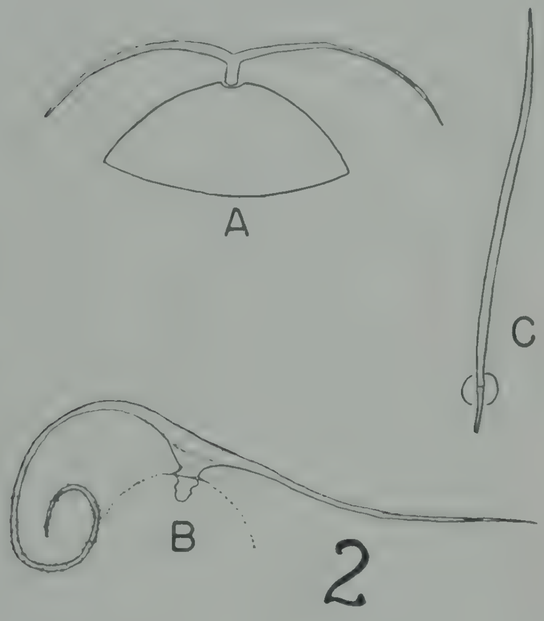

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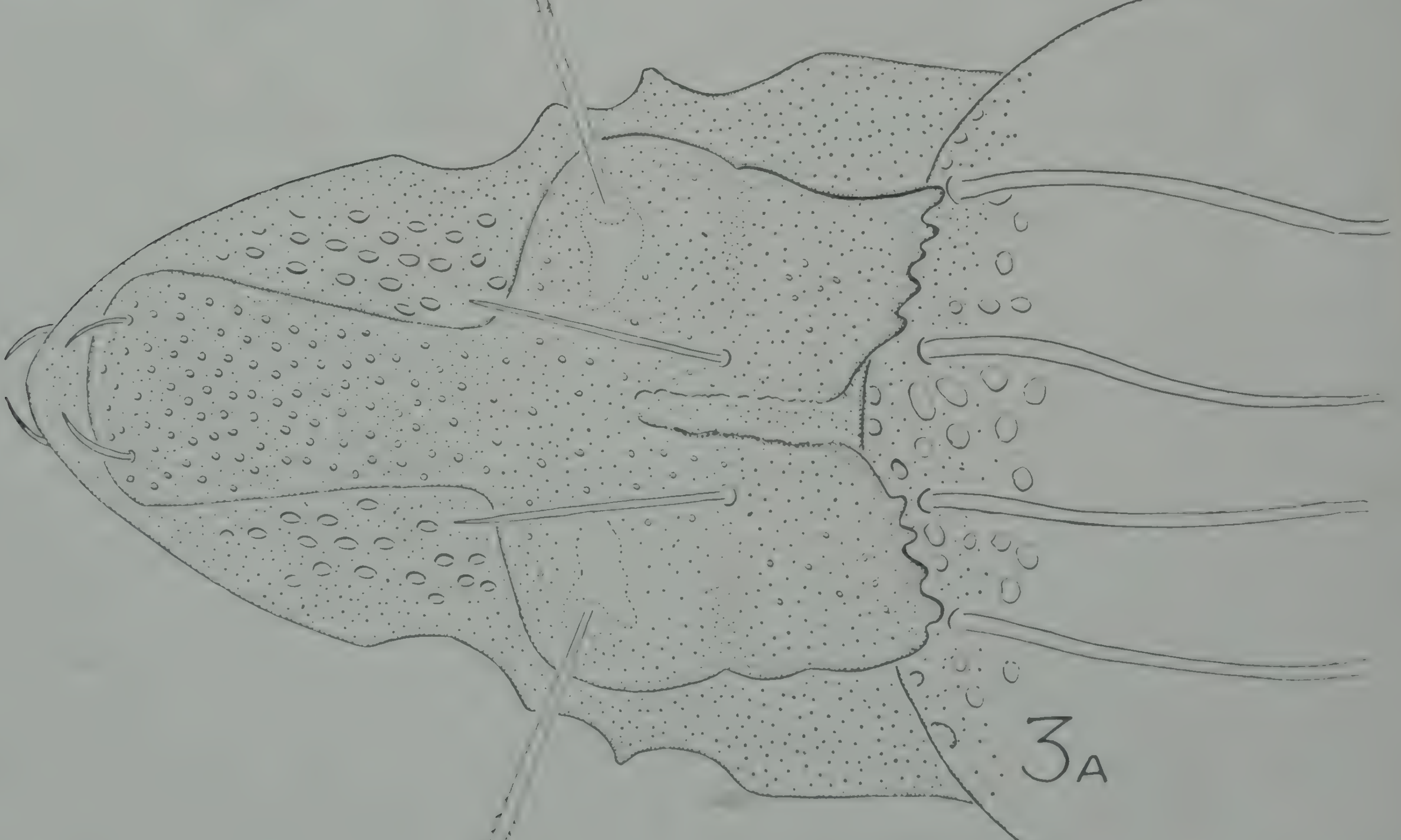


3A

Fig. 1. Propodosoma of *Nanhermannia comitalis* Berlese, from the dorsal aspect; A, bifurcate seta on genu and tibia I (after Willmann, 1931).

Fig. 2. Types of T-shaped setae in (A) *Masthermannia*, (B) *Posthermannia* and (C) *Nanhermannia*.

Fig. 3. Propodosoma and anterior part of hysterosoma of *Masthermannia mammillaris* Berlese from dorsolateral aspect (after Berlese, 1913).

Fig. 3a. Propodosoma of *Nanhermannia komáreki* Kunst from the dorsal aspect (after Kunst, 1956).

characters and that the setae, posterior propodosomal apophyses and other features are apparent anatomical evidences of familial relationship between *Masthermannia*, *Nanhermannia*, and *Posthermannia*. These observations are corroborated to some extent by the findings of Grandjean (1953) concerning the nymphal characters of *Nanhermannia* and *Masthermannia*.

As a result of these observations, the writers are convinced that certain taxonomic revisions should be made within the family Nanhermanniidae and that the genus *Masthermannia* should be included in this group. These changes are delineated below.

There are numerous references which contain information on the family Nanhermanniidae. The most recent works are those of Grandjean (1953, 1954), Strenske (1953), Turk (1953), Evans (1952) and van der Hammen (1952). The reader is referred to these articles for taxonomic or ecologic details other than those incorporated in the following text. Most of the descriptions of species of *Nanhermannia* are modified from the excellent paper by Strenske (1953). Papers by Berlese (1904, 1913, 1916), Michael (1888, 1898), Sellnick (1928) and Willmann (1931) were also consulted.

Family NANHERMANNIIDAE Sellnick, 1924

Type genus: *Nanhermannia* Nicolet, 1855, p. 458.

Diagnosis: Elongated mites with a ventral crescentic suture between propodosoma and hysterosoma; narrow, sac-like hysterosoma; mid-dorsal surface of propodosoma with T-shaped area, consisting of a lamellar part as base of a T, and an interpseudostigmatic cross-bar, forming the arms of a T, variously sculptured; posterior margin of propodosoma usually with sclerotized serrate or dentate apophyses extending over anterior border of hysterosoma; setae usually T-shaped, although one arm of T may be reduced to a minute spur at base of main seta in setal insertion; genital aperture contiguous with apodemata IV, separated from anal aperture by crescentic hysterosomal suture; nine pairs of genital setae; anal aperture contiguous with posterior ventral margin of hysterosoma.

Description: Chelicerae chelate, propodosoma narrowly triangular, rostrum blunt or rounded, rostral hairs usually simple, inserted in slight prominences at antero-lateral margins of rostrum. Hairs of propodosoma simple or T-shaped. Lamellar hairs inserted in lamellar part of T-area, inter-lamellar hairs inserted in inter-pseudostigmatic cross-bar. Pseudostigmata raised, dorso-lateral cylinders or prominences; pseudostigmatic organs bristle-like, serrate at tips. Ventro-lateral margins of propodosoma variously notched, surface variously sculptured. Posterior margin of propodosoma usually sclerotized, divided medially by a groove or notch and with projecting serrate or dentate apophyses on each side of notch; apophyses usually extending over anterior border of hysterosoma. Surfaces of propodosoma and hysterosoma variously pitted or sculptured. Ventral crescentic suture between propodosoma and hysterosoma curved mediad from level of leg IV to nearly encompass genital aperture posteriorly, medial tips of suture separated by half the width of genital opening; as seen from lateral aspect, suture is curved ventrad from anterior margin of hysterosoma to approximate dorsal margin of insertion of leg IV, ending near posterio-lateral margin of genital aperture. Hysterosomal setae T-shaped, simple with small basal spur or with short base and long or short arms. Genital aperture subglobose, each genital cover with nine setae along medial margin. Anal aperture contiguous with posterior margin of hysterosoma, two anal setae and a glandular fissure (?) on each anal cover.

Genus *Nanhermannia* Berlese, 1913

Type: *Nothrus nanus* Nicolet, 1855, p. 458.

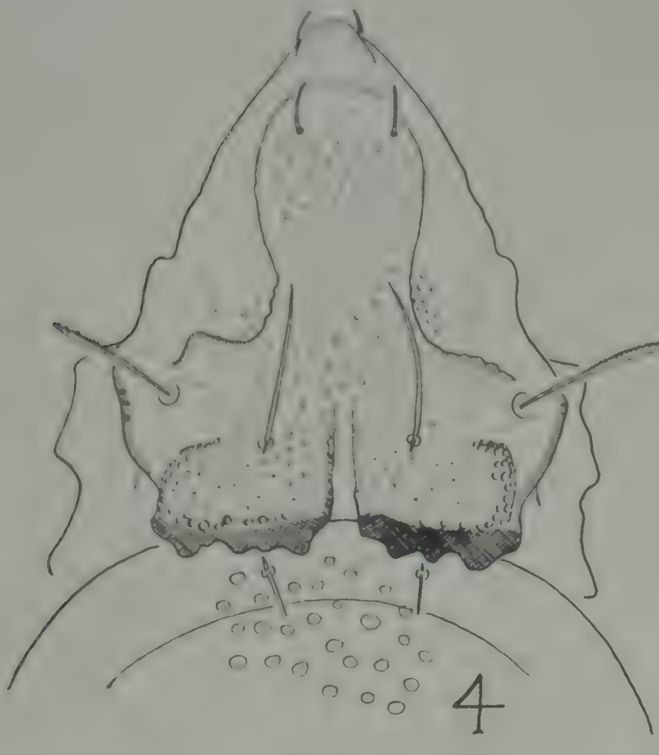
Diagnosis: Propodosomal and hysterosomal setae and setal insertions simple; setae with a fine basal spur; posterior margin of propodosoma usually with sclerotized dentate or serrate apophyses which extend over anterior end of hysterosoma.

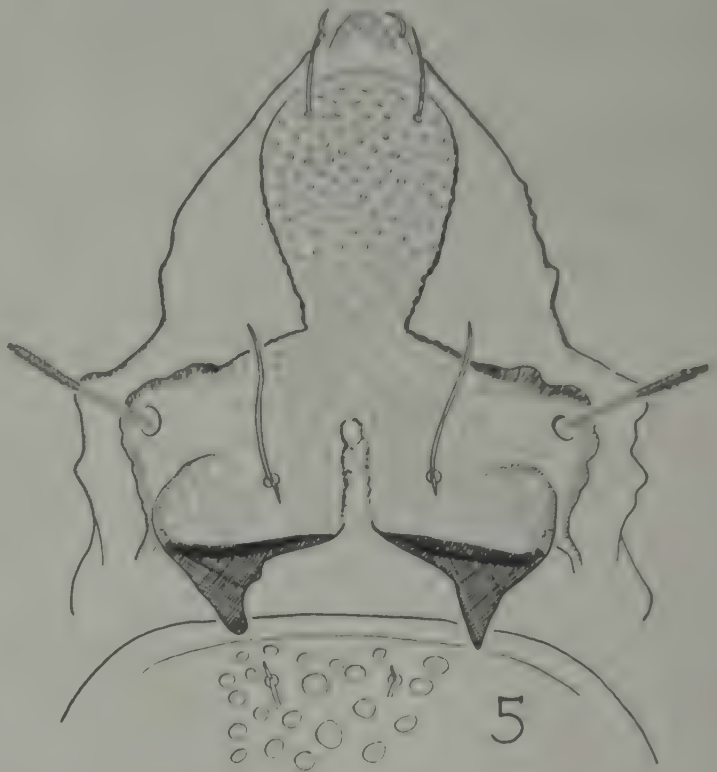
Nanhermannia nana (Nic., 1855) Berlese, 1913

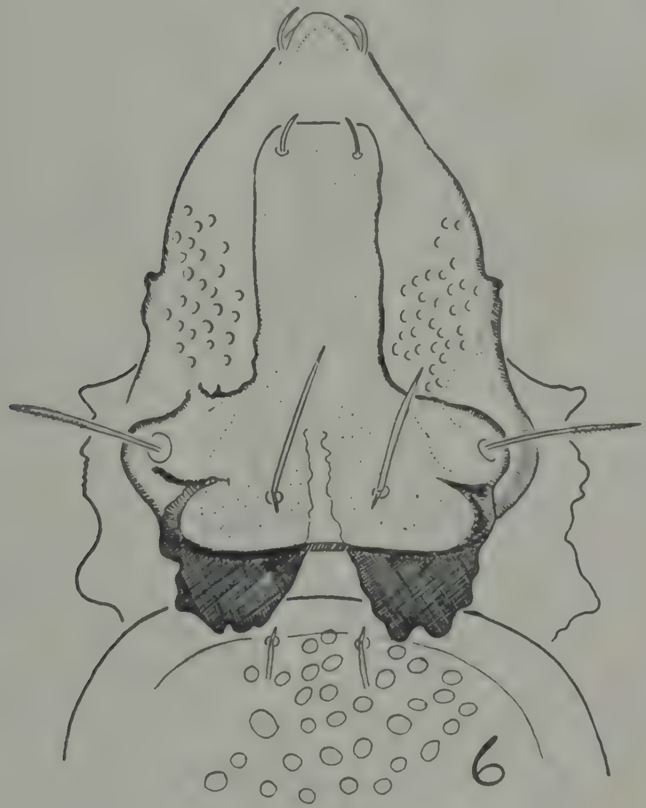
Fig. 4

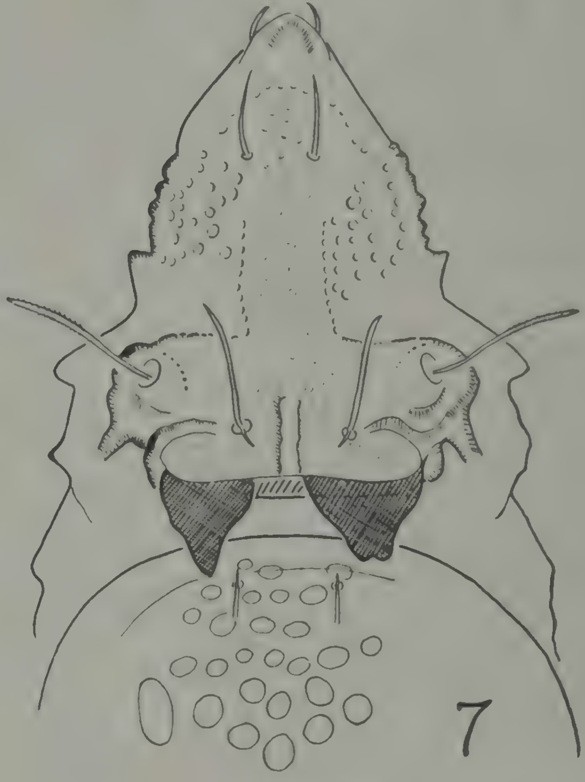
Nothrus nanus Nic., 1855, p. 458.
Hermannia nanus Michael, 1888, p. 455.
Nanhermannia nana Berlese, 1913, p. 100; Sellnick, 1928, p. 17; Willmann, 1931, p. 96; Strenske, 1953, p. 74.

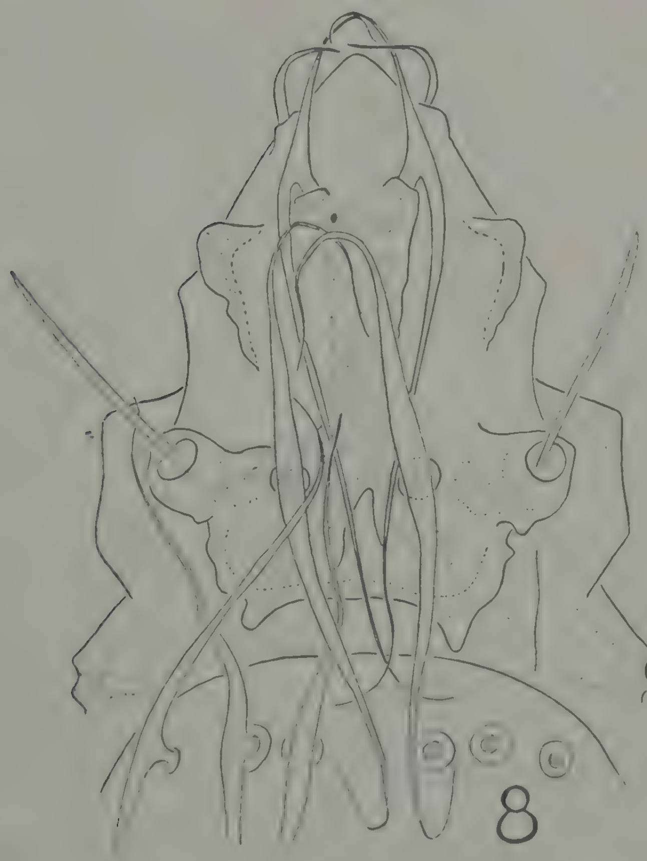
Diagnosis: Lamellar part of T-area rounded anteriorly, surface slightly punctate; posterior propodosomal apophyses with broadly notched margin which slightly overlaps anterior border of hysterosoma.











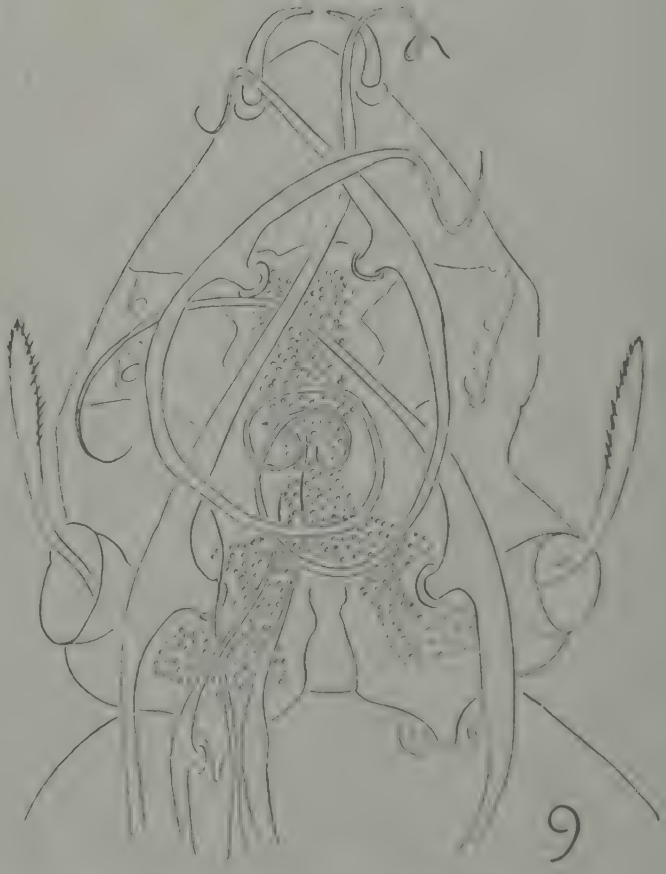


Fig. 4. Propodosoma of *Nanhermannia nana* Berlese from the dorsal aspect (after Strenske, 1953).

Fig. 5. Propodosoma of *Nanhermannia elegantula* Berlese from the dorsal aspect (after Strenske, 1953).

Fig. 6. Propodosoma of *Nanhermannia pectinata* Strenske from the dorsal aspect (after Strenske, 1953).

Fig. 7. Propodosoma of *Nanhermannia areolata* Strenske from the dorsal aspect (after Strenske, 1953).

Fig. 8. Propodosoma of *Posthermannia nematomorpha* Grandjean from the dorsal aspect (after Grandjean, 1954).

Fig. 9. Propodosoma of *Posthermannia hirsuta* (Hartman) from the dorsal aspect (after Hartman, 1949).

DESCRIPTION: Rostal hairs short, curved, inserted about twice their lengths apart on antero-lateral aspects of propodosoma. Lamellar hairs only slightly longer than rostral hairs, inserted in round corners of lamellar part of T-area, about twice the length of one hair apart. Lamellar part of T-area rounded anteriorly, lateral margin shallowly indented antero-mesad of pseudostigmata, surface with shallow pits and granulations. Lateral margin of propodosoma slightly notched. Pseudostigmata in extreme ends of interpseudostigmatic cross-bar. Pseudostigmatic organs bristle-like, setose at distal tips, directed antero-laterad. Interlamellar hairs simple, longer than pseudostigmatic organs, directed forward from insertions which lie mesad and posterior to pseudostigmata. Posterior apophyses with a broadly notched margin which extends very slightly over anterior border of hysterosoma.

Michael (1898) mentions that this species is "dark reddish brown, rough, dull, coarsely pitted . . . dorsum of abdomen very arched with 8 longitudinal rows of white, rod-like hairs."

Length 525mu, width 253 mu.

DISCUSSION: Michael (1888, 1889) indicates that this species is found in England, France and Italy. Forsslund (1939) and Evans (1952) mention the species as a resident of the F and H layers of soil in Sweden and England, respectively. Strenske (1953) relates that *N. nana* is common to all of Europe, Italy to Finland, Swedish Lappland and North America. van der Hammen (1952) describes this mite from moist habitats near Mantinge, Netherlands. He indicates that this species appears to have more of a preference for damp areas than does *N. elegantula*. Of the two he found *N. nana* less frequently in forest litter. Specimens of *N. nana* were obtained by the writers at Patuxent, Md., 22 June 1954, and from Mt. Si, Washington, 28 June 1956, by Marie Higgins.

Nanhermannia elegantula Berlese, 1913

Fig. 5

Nanhermannia elegantula Berlese, 1913, p. 100; Sellnick, 1928, p. 17; Willmann, 1931, p. 96; van der Hammen, 1952, p. 10; Strenske, 1953, p. 72.

DIAGNOSIS: T-area of propodosoma distinctly outlined, broadly rounded anteriorly, surface pitted and granulated; posterior propodosomal apophyses long, conical teeth, extending over anterior margin of hysterosoma.

DESCRIPTION: Rostrum blunt, with a rounded medial projection, rostral hairs simple, sharply decurved, inserted in prominences lateral to medial projection. Lamellar hairs simple, decurved, twice as long as rostral hairs, inserted in antero-lateral corners of lamellar part of T-area. T-area with distinct border; lamellar part rounded anteriorly, nearly as wide as width of propodosoma at level of lamellar hairs, narrowed abruptly adjacent to interpseudostigmatic cross-bar; surface sculptured with small pits and fine granulations, pits reduced in size between interlamellar hairs. Pseudostigmata in antero-lateral corners of interpseudostigmatic cross-bar. Pseudostigmatic organs bristle-like, setose at distal tips, about as long as interlamellar hairs. Interlamellar hairs inserted posterior to level of pseudostigmata, slightly longer than pseudostigmatic organ, curved at tips. Posterior propodosomal apophyses separated by prominent groove; each apophysis a single, pointed tooth, tip extended over anterior margin of hysterosoma.

Length 510 mu, width 215 mu.

DISCUSSION: Berlese (1913) records this species in detritus and humus near Tiarno, Italy. van der Hammen (1952) indicates collections of *N. elegantula* in forest soils of various areas of the Netherlands. Strenske's findings (1953) extend the range of the species from Italy to southern Sweden and demonstrate that it may be found in saline woods along the sea coast. The writers have specimens of this species from Duke Forest, N. C.; Preston, Idaho; Bellevue, Colorado; and Mt. Si, Washington.

Nanhermannia comitalis Berlese, 1916

Fig. 1

Nanhermannia comitalis Berlese, 1916, p. 335; Sellnick, 1928, p. 17; Willmann, 1931, p. 96.

DIAGNOSIS: T-area of propodosoma unsculptured, finely granulate; posterior propodosomal apophyses without ornamentation; a triangular, forked seta on genu and tibia I and II.

Description: Rostrum blunt, rounded, rostral hairs short, inserted in anterior margin. Lamellar hairs inserted in anterior margin of T-area, about twice as long as rostral hairs. Lateral surfaces of propodosoma without pits, margins entire, not notched. Interlamellar hairs straight, slightly longer than pseudostigmatic organs, inserted between pseudostigmata in interpseudostigmatic cross-bar. Posterior propodosomal apophyses without ornamentation. Surface of hysterosoma finely pitted. A triangular, forked seta on genu and tibia I and II.

Length 660 mu, width 340 mu.

Discussion: van der Hammen (1952) records specimens of this species from a wet hayfield in Maasland, Netherlands, and considers it rare and new to the fauna of that country. He uses the size of the body and the depth and distribution of the hysterosomal pores in preference to the forked setae for the differentiation of *N. comitalis* and the distinction between *N. elegantula* and *N. nana*. The writers have no specimens of *N. comitalis* in their collections nor were they able to obtain representatives for observation. The description is summarized from the literature.

Nanhermannia pectinata Strenske, 1953

Fig. 6

Nanhermannia pectinata Strenske, 1953, p. 71.

Diagnosis: Lamellar part of T-area with parallel sides, surface granulate; posterior propodosomal apophyses with 4 or 5 short teeth, projected over anterior margin of hysterosoma.

Description: Rostrum blunt, rostral hairs curved, inserted in dorso-lateral margins of rostrum. Lamellar hairs short, about as long as rostral hairs, curved, inserted in antero-lateral corners of lamellar part of T-area. Antero-lateral margins of propodosoma nearly smooth, with one or two short projections, surface lateral to T-area with shallow pits, T-area finely granulate, lamellar part with parallel margins, about same width as distance between insertions of interlamellar hairs. Pseudostigmata in rounded ends of interpseudostigmatic cross-bar. Pseudostigmatic organs bristle-like setose at distal tips, directed laterad, about as long as interlamellar hairs. Interlamellar hairs inserted between pseudostigmata, slightly posterior to level of pseudostigmatic opening, a medial groove between insertions. Posterior propodosomal apophyses with serrate margins of 4–5 well developed, sclerotized teeth, extending over anterior margin of hysterosoma.

Length 560 mu, width 224 mu.

Discussion: Collected by Strenske (1953) in Buchenwald, Holstein, Germany, 18 May 1940, this species resembles *N. dorsalis* (Banks, 1896) Jacot, 1937, but is not considered synonymous with the latter because of the parallel base of the T-area on the propodosoma and the bristle-like pseudostigmatic organs. The writers did not see specimens of this species.

Nanhermannia areolata Strenske, 1953

Fig. 7

Nanhermannia areolata Strenske, 1953, p. 69.

Diagnosis: T-area of propodosoma weakly developed, indistinctly outlined, granulate; posterior propodosomal apophyses pointed and conical, sometimes slightly notched or bifurcate, extended over anterior margin of hysterosoma.

Description: Rostrum blunt, rostral hairs inserted in anterior margin. Lamellar hairs curved, inserted their lengths from lateral edges of propodosoma, slightly incurved at tips. Lateral margins of propodosoma serrate, surfaces pitted lateral to T-area. T-area with indistinct margins, finely granulate, weakly pitted with parallel sides adjacent to interpseudostigmatic cross-bar. Pseudostigmata in sclerotized lateral margins of interpseudostigmatic bar. Pseudostigmatic organs slightly longer than interlamellar hairs, projected antero-laterad, setose along distal tips. Interlamellar hairs simple, erect, slightly shorter than pseudostigmatic organs, inserted posterior to level of pseudostigmata, with a slight groove between insertions. Posterior propodosomal apophyses cone-like with one or two points, stout, blunt, connected by a sclerotized bar at base, slightly overlapping anterior margin of hysterosoma.

Length 535 mu, width 216 mu.

Discussion: This species differs from *N. elegantula* in a granulate, indistinct lamellar part of the T-area and in a pitted propodosomal surface. Strenske (1952) collected this species in Preetz, Holstein, Germany, May 1940. Fourteen specimens of *N. areolata* Strenske were collected at Parvin Lake, Colorado, 13 June 1955, by Dale Hoffman. Most of these specimens show minor variations of the posterior propodosomal apophyses. Many of them exhibit bifurcate tips, but the writers assume these to be individual variations and not morphological features of a specific nature.

Nanhermannia komáreki Kunst, 1956

(Fig. 3a)

Nanhermannia komáreki Kunst, 1956, p. 267.

Diagnosis: T-area of propodosoma distinct, wider anteriorly between lamellar hairs, narrowed near interpseudostigmatic cross-bar, with numerous shallow pits in lamellar part, pits sparsely distributed in cross-bar. Posterior propodosomal apophyses serrate, with longer lateral extensions than medial points on each apophysis.

Description: Rostrum pointed, rostral hairs short, decurved. T-area of propodosoma distinct; lamellar part broadest between lamellar hairs, narrowed near interpseudostigmatic cross-bar; with numerous shallow pits and bare areas, pits fewer and smaller in cross-bar. Latero-dorsal surface of propodosoma with large pits, margins indented for insertions of leg I. Pseudostigmata cornuate beneath surface of cross-bar, pseudostigmatic organ stout, straight, thickened at distal tip, setose. Posterior propodosomal apophyses serrate, lateral extensions longer than medial points on each apophysis.

Hysterosoma with shallow depressions in integument, depressions not as large as in *N. elegantula*, but wider and more distinct than *N. nana*. Bristles of hysterosoma longer than those of latter two species, ending in a long tapered point, averaging 150 mu in length.

Length 535–620 mu, width 238–297 mu, average 272 mu.

Discussion: According to Kunst (1956) a holotype and 32 paratypes of the species were collected (18/8/54, 25/7/55) with other mites near Ceska Trebova, Bohemia. The species is described as larger than *N. elegantula*, with differences in hysterosomal hairs, apophyses and integumental pitting. The writers were able to insert this species in the revision through the kindness of Dr. Kunst, who sent a reprint of his article in October, 1956. This species was not included in the presentation by the senior author at the Tenth International Congress of Entomology at Montreal, Canada, August, 1956.

SPECIES OF UNCERTAIN POSITION

Nanhermannia fluviatilis (Hull, 1913) Turk, 1953

Hull (1913) describes the features of this species as intermediate between *Hermannia* convexa (Koch) and *H. bistriata* (Nic.), but indicates that the size is larger than either. The respective lengths of the latter species are 1,350 mu and 620 mu. If *N. fluviatilis* is larger than either of these species, its length is more than double the longest known measurement for *Nanhermannia*. Turk (1953) lists *N. fluviatilis* with other species of *Nanhermannia* and justifies the name on the basis of a notation by J. E. Hull on the slide of the specimen concerned. The writers consider that the length measurements, the differences in pseudostigmatic organs and the marginate dorsum of the hysterosoma contradict the inclusion of this species in the genus *Nanhermannia*.

Nanhermannia dorsalis (Banks, 1896) Jacot, 1937

? (= *Nanhermannia coronata* Berlese, 1913).

Jacot (1937) suggests that Banks' species (*Carabodes dorsalis*) is the same as the one described by Berlese from Lake City, Florida. Hartman (1949) makes *N. dorsalis* (Banks) a synonym of *N. nana* Berlese. van der Hammen (1952) relates *N. dorsalis* to *N. nana*, but indicates differences in the pores and size of propodosomal apophyses. Strenske (1953) also discusses the uncertain position of these species.

There is no doubt that Banks' description makes his *Carabodes dorsalis* a species of *Nanhermannia* because of the T-mark on the propodosoma. This change was effected by Jacot (1937). Since it was impossible to obtain specimens of these species for comparison, however, the writers defer exact placement until such time as examples may be examined and the specific position determined.

Genus *Masthermannia* Berlese, 1913

Type: *Angelia mammillaris* Berlese, 1903.

DIAGNOSIS: Lamellar hairs and setae of hysterosoma T-shaped, arms of T short, subequal, setae inserted in raised, swollen tubercles, posterior margin of propodosoma without dentate apophyses.

Masthermannia mammillaris Berlese, 1913

Fig. 3

Angelia mammillaris Berlese, 1903, p. 275.
Masthermannia mammillaris Berlese, 1913, p. 100; Baker and Wharton, 1952, p. 405, fig. 331.

DIAGNOSIS: Rostral and interlamellar hairs simple, lamellar hairs T-shaped; posterior margin of propodosoma without projecting apophyses; setae of hysterosoma T-shaped, arms of T short, subequal, setae inserted in swollen, raised tubercles.

DESCRIPTION: Blackish, elongate; lateral margins of propodosoma angular; rostrum rounded, rostral bristles straight, short, about their length apart. Lamellar hairs T-shaped, inserted in prominent tubercles at anterior corners of lamellar area. Pseudostigmata prominent, cylindrical, projected antero-laterad above conical propodosoma. Pseudostigmatic organ long, filiform. Interlamellar hairs simple, straight, about as long as distance between insertions.

Hysterosoma somewhat angular, dorsum with prominent swollen tubercles in which T-shaped setae insert. Surface of hysterosoma thickly reticulate around tubercles. Legs bearing foliate hairs, tarsi monodactyle.

Length 400 mu, width 200 mu.

DISCUSSION: Berlese (1904) indicates that the propodosoma is conical, somewhat sculptured and with an ornate crest. The crest does not show in his figure, but there may be a similarity between this crest and the T-area on the propodosoma, so typical of other members of this family. Baker and Wharton (1952) indicate this species in Hermanniidae.The presence of T-shaped setae, however, and the shape and ornamentation of the propodosoma, the reticulations and form of the hysterosoma validate, in the opinions of the writers, the inclusion of this species in the family Nanhermanniidae. Berlese's several specimens, all adult females, were collected in humus and moss near Florence, Italy. The authors did not see nor collect specimens of this mite. Their inferences are based strictly on evidences from the literature.

Genus *Posthermannia* Grandjean, 1954

Type: *Posthermannia nematomorpha* Grandjean, 1954, p. 298.

DIAGNOSIS: Rostral hairs simple; other propodosomal and hysterosomal setae T-shaped, with short base and long, tenuous arms, inserted in swollen tubercles, three setae inserted in posterolateral tubercle (h3 of Grandjean). Propodosoma with sclerotized, pointed posterior apophyses.

Posthermannia hirsuta (Hartman), 1949

Fig. 9

Nanhermannia hirsuta Hartman, 1949, p. 169.

DIAGNOSIS: Rostral hairs simple, heavy, lamellar and interlamellar hairs T-shaped; setae of hysterosoma T-shaped with long tenuous arms, setae of hysterosoma inserted in swollen tubercles; integument with pentagonal depressions; pseudostigmatic organs slightly clavate, setose at tip. Propodosomal apophyses projected over anterior margin of hysterosoma.

DESCRIPTION: Rostrum pointed, rostral hairs as long as distance between insertions, incurved and tapered, inserted on anterolateral angle of propodosoma. Lamellar hairs T-shaped, inserted in corners of lamellar part of T-area of propodosoma. Surface of propodosoma lateral to lamellar hairs with a prominent sclerotized projection. Pseudostigmata short cylinders laterad of interlamellar hairs. Pseudostigmatic organ simple, setose at tip, extended anterodorsally. Posterior propodosomal apophyses consisting of a single tooth each side, a deep groove or cleft between, apophyses overlapping anterior margin of hysterosoma.

Hysterosoma with 13 pairs of T-shaped setae inserted in tubercles, posterior arm of T unbarbed, tenuous. Surface of hysterosoma with pentagonally reticulate, shallow pits of varying size. Venter with a crescentic suture between genital and anal apertures.

Length 453 mu, width 220 mu.

Discussion: *Posthermannia hirsuta* is smaller than *P. nematomorpha* and differs principally in the rostral hairs, pseudostigmata, pseudostigmatic organs, arrangement of the propodosomal T-area and the pentagonal areas of the hysterosomal integument. The posterior propodosomal apophyses are similar in both species, but the apophyses and the groove between appear to be more developed in *P. hirsuta*, in which the apophyses also project over the anterior margin of the hysterosoma. It is possible, however, that the projection of the apophyses in this manner may be somewhat relative, depending upon the preparation and mounting of the specimen, or the pressure of the medium.

According to Dr. Baker, the type specimen of this species is mounted in PVA, which has compressed the mite and flattened the setal tubercles.

Hartman (1949) described a single specimen which was obtained from an armadillo nest by J. V. Irons, 17 January 1948, in Travis County, Texas.

Posthermannia nematomorpha Grandjean, 1954

Fig. 8

Posthermannia nematomorpha Grandjean, 1954, p. 298.

Diagnosis: Lamellar, interlamellar and hysterosomal setae T-shaped; hysterosomal setae inserted in swollen tubercles, posterior arm of T-shaped setae barbed; integument of hysterosome with shallow pits of irregular outline. Pseudostigmatic organ filiform. Propodosomal apophyses not projected over anterior margin of hysterosoma.

Description: Rostrum pointed, rostral hairs simple, longer than distance between insertions, incurved and tapered. Lamellar hairs T-shaped, inserted in antero-lateral corners of lamellar part of T-area. Propodosoma with triangular dorso-lateral projections slightly posterior to level of lamellar hairs. T-area granulate, interpseudostigmatic cross-bar with posterior medial groove; interlamellar hairs T-shaped, inserted between pseudostigmata. Pseudostigmata stout, cylindrical projections at lateral tips of interpseudostigmatic cross-bar. Pseudostigmatic organs lanceolate, setose distally, projected forward and laterad. Posterior propodosomal apophyses conical, left one smaller than right, neither point reaching anterior border of hysterosoma.

Hysterosoma with 13 pairs of T-shaped setae, inserted in swollen tubercles, posterior arm of each T-shaped seta barbed. Integument with shallow pits of irregular size and shape.

Length 465–485 mu.

Discussion: The reader should consult Grandjean (1954) for additional details concerning setae, solenidions and nymphal structures. His careful and meticulously executed drawings and verbal descriptions demonstrate details which are interesting, but which cannot be reproduced in this paper. Three adults, four tritonymphs and one protonymph were collected by Grandjean in March of 1927 near Ales (Gard), France.

Key to the Genera and Species of Nanhermanniidae

Elongated, sac-like mites; usually with a T-shaped area on dorsum of propodosoma; a ventral, crescentic suture and nine pairs of genital setae . . . Family Nanhermanniidae Sellnick, 1924.

1. Setae of hysterosoma simple, with a minute basal spur, not inserted in swollen tubercles . . . . Genus *Nanhermannia* Berlese, 1913 2
Setae of hysterosoma prominently T-shaped, usually inserted in swollen tubercles . . 7

2. Posterior margin of propodosoma with points or serrations, genu and tibia I & II without forked seta 3
Posterior margin of propodosoma without points or apophyses, genu and tibia I & II with forked seta . . . . *comitalis* Berlese, 1916

3. Posterior propodosomal apophyses with one or two points on each side 4
Posterior propodosomal apophyses notched or serrate, with more than 2 points on each side 5

4. Lamellar (mid-dorsal) part of T-area rounded anteriorly and sculptured, latero-dorsal surface of propodosoma smooth . . . . *elegantula* Berlese, 1913
Lamellar (mid-dorsal) part of T-area with parallel sides, indistinct anteriorly, latero-dorsal surface of propodosoma sculptured . . . . *areolata* Strenske, 1953

5. Lateral margins of lamellar (mid-dorsal) part of T-area tapered or rounded, surface with pits 6
   Lateral margins of lamellar (mid-dorsal) part of T-area parallel, surface finely stippled, without pits. . . . . *pectinata* Strenske, 1953
6. Lateral margins of lamellar (mid-dorsal) part of T-area evenly tapered, unequal dispersion of integumental pits in T-area, teeth of posterior propodosomal apophyses relatively long, hysterosomal setae with long, tapered point (150 mu). . . . . *komáreki* Kunst, 1956
   Lateral margins of lamellar (mid-dorsal) part of T-area broadly rounded anteriorly, equal dispersion of integumental pits in T-area, teeth of propodosomal apophyses short, knobby, with pits in dorsal surfaces, hysterosomal setae not longer than 140 mu . . . . *nana* (Nic., 1855) Berlese, 1913
7. Tshaped setae with short, subequal arms, single seta in a tubercle . . . . *Masthermannia mammillaris* Berlese, 1913
   T-shaped setae with long, tenuous arms, 3 setae inserted in postero-lateral tubercle (h3) on hysterosoma . . . . Genus *Posthermannia* Grandjean, 1954 8
8. Integument with shallow pits of irregular outline, propodosomal apophyses not extended over anterior margin of hysterosoma, posterior arm of T-shaped seta barbed . . . . *nematomorpha* Grandjean, 1954
   Integument with pentagonal reticulations, propodosomal apophyses extended over anterior margin of hysterosoma, posterior arm of T-shaped seta smooth . . . . *hirsuta* (Hartman), 1949

SUMMARY

The ventral crescentic suture constitutes one of the best evidences of familial relationship between *Nanhermannia* and *Posthermannia*. This suture is suspected for *Masthermannia*, but since it is not proven at this time, the characteristic cannot be used to justify placement in the family Nanhermanniidae. In the absence of this convincing feature, however, there are other characters which are considered by the writers to vindicate the inclusion of *Masthermannia* in the family.

The presence of similar T-shaped setae inserted in swollen tubercles in both *Masthermannia* and *Posthermannia* suggests a close generic relationship which surmounts the lack of proof regarding a crescentic suture. All the illustrated species of *Nanhermannia* exhibit setae with a basal spur, indicative of modification of a T-shaped seta. The writers acknowledge that there are minor variations in these setae, but they assume that since the setae of *Masthermannia* resemble those of *Posthermannia* and both *Posthermannia* and *Nanhermannia* demonstrate crescentic sutures, all of these mites are related.

One also observes similarities in the pseudostigmata and pseudostigmatic organs of these three genera. The pseudostigmata of *Masthermannia* are tubular and prominently project from the sides of the propodosoma. The pseudostigma of *Posthermannia* demonstrate a reduction of the tubular aspect. This reduction is emphasized in the species of *Nanhermannia* where the pseudostigmata are cylindrical sclerotizations within the lateral extensions of the interpseudostigmatic cross-bars. The pseudostigmata appear to exhibit a transitional change from the prominent cylinders of *Masthermannia* through the intermediate reduction in size of the cylinders in *Posthermannia* to the culmination of this reduction in *Nanhermannia*.

The apparently pronounced transitional development of pseudostigmata in these three genera is not accompanied by structural modification in the pseudostigmatic organs. The pseudostigmatic organs are quite similar in all species of the family except for *P. hirsuta*, in which the proportions may have been slightly overemphasized in the illustration of the organs. All of the pseudostigmatic organs in the species of the three genera are lanceolate and appear setose at their distal tips.

Developmental changes in the posterior propodosomal apophyses are apparent in the genera of this family. Berlese's figure of *Masthermannia* demonstrates a lack of these structures. All of the remaining species of the family as now constituted demonstrate the apophyses, but with a developmental and transitional pattern just the reverse of the pseudo-

stigmata. The lack of apophyses places *Masthermannia* at one extreme of development, *Posthermannia* intermediate, and the species of *Nanhermannia* in the situation in which the apophyses are most highly developed.

The most interesting variations occur in the T-area of the propodosoma, in which transitional intrageneric development seems to have taken place in *Posthermannia* and *Nanhermannia*. It seems to be especially emphasized in the species of the latter genus, where both expansion and reduction of the lamellar part of the T-area are accompanied by similar variations of the posterior propodosomal apophyses in two sets of species. It is difficult to determine which of the two conditions of the lamellar variation constitutes specialization. The striking phenomenon is that the expanded (bulging) condition of the lamellar T-area accompanies both serrate and pointed apophyses, as does the reduced (parallel) condition of this same area. Perhaps this is an exhibition of similar divergence along two interspecific lines.

The most general of the similarities of these three genera is found in the sac-like hysterosoma. Many of the oribatids demonstrate rotund or oval hysterosomas and the writers admit that there are similarities between familial groups in this respect. They are convinced, on the other hand, that the general hysterosomal shape of *Masthermannia* belies its present placement in the family Hermanniidae.

The writers acknowledge that minor variations will be noted in a comparison of the species which have been included in the revision of Nanhermanniidae. They conclude, however, that the genus *Masthermannia* is a logical representative of this group and that this genus is justifiably related to *Posthermannia* and *Nanhermannia* in the family Nanhermanniidae.

REFERENCES

Baker, Edward W., and G. W. Wharton. 1952. An introduction to acarology. New York: *Macmillan*, xiii+ 465 pp., 377 figs.

Berlese, A. 1904. Acari nuovi. *Redia* 1: 259–280.

Berlese, A. 1913. Acari nuovi. *Redia* 9: 77–111.

Berlese, A. 1916. Centuria terza di Acari nuovi. *Redia* 12: 289–338.

Evans, G. O. 1952. Terrestrial Acari new to Britain. *Ann. & Mag. Nat. Hist.* 5: 33–41.

Forsslund, Karl-Herman. 1939. Uber die Ernährungsverhältnisse der Hornmilben (Oribatiden) und ihre Bedeutung für die Prozesse im Waldboden. *Internat. Kong. f. Entom., Berlin* 3: 1950–1957.

Grandjean, F. 1953. An attempt to classify the Oribatidae (Acarina). *Bul. Soc. Zool. de France* 78(5–6): 421–466.

Grandjean, F. 1954. *Posthermannia nematomorpha* n.g., n. sp. *Revue Française d'Entomologie* 21(4): 298–311.

van der Hammen, L. 1952. The Oribatei (Acari) of the Netherlands. *Zool. Verhandelingen* No. 17: 139 pp.

Hartman, A. G. 1949. A new species of *Nanhermannia* with notes on the genus. *Proc. Ent. Soc. Wash.* 51(4): 169–171.

Hull, J. E. 1914. Oribatidae of the County of Durham with special reference to the Derwent Valley. *Trans. Vale Derwent Nat. F. Cl.* 1: 59–65.

Jacot, A. P. 1937. New moss mites—chiefly midwestern. II. *Amer. Midl. Nat.* 18(2): 237–250.

Kunst, Miroslav. 1956. *Nanhermannia komáreki* n. sp., eine neue Oribatiden-Art aus Böhmen. *Acta Societatis Zoologicae Bohemoslovenicae* XX(3): 267–272.

Michael, A. D. 1888. British Oribatidae. Vol. 2. *Ray Society* 1887: 337–667.

Michael, A. D. 1898. Oribatidae. Das Tierreich. Vol. 3: 1–93.

Sellnick, Max. 1929. Formenkreis: Hornmilben, Oribatei. *In* Tierwelt Mitteleuropas. 3(3/4): 1–42.

Strenske, Karl. 1953. Zwei neue Arten der Oribatiden-Gattung *Nanhermannia*. *Zool. Anz.* 150(3/4): 69–75.

Turk, F. A. 1953. A synonymic catalogue of British Acari. *Ann. & Mag. Nat. Hist.* 6(62): 81–99.

Willmann, Carl. 1931. Moosmilben oder Oribatiden (Oribatei). *In* Tierwelt Deutschlands 22(5): 79–200.

The Reproduction of Chigger-Mites (Acarina: Trombiculidae)

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ABSTRACT[1]

Studies of chigger reproduction carried out at Walter Reed Army Institute of Research, Washington, D.C., have demonstrated that fertilization of female chiggers is accomplished not by copulation, as was previously supposed, but by means of spermatophores. Close observation of the adult chiggers revealed the method of deposition of spermatophores by males and the method of utilization of them by females. Spermatophores consist of a spherical portion, containing the sperm, and a supporting filament, drawn from a ductile basal mass of material. The spermatophores of four species studied showed characteristic differences in shape.

Experimental observation series of Trombicula (Eutrombicula) splendens *Ewing were established to provide quantitative data on spermatophores. All females used in these series were reared in isolation. Of 35 control females maintained in isolation, 20 produced no eggs during a period of 50 days, while the remaining 15 failed to oviposit for over 200 days. Of 20 females kept together with males, 18 laid eggs within 33 days. In a series of 20 females exposed to about ten spermatophores each, 17 produced eggs, one, however, as long as 81 days following initial exposure. Twenty females were exposed to a single spermatophore each, with the result that 10 subsequently laid eggs, although one of these females did not commence laying until 107 days following exposure to the spermatophore. Larvae hatched from eggs of each productive female.*

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[1] See the following reference for the full text. Spermatophores—the mode of insemination of chiggers (Acarina: Trombiculidae). *Jour. Parasitol.* 43(3): 256–262. 1957.

New Ideas on the Genus Bryobia (Acari, Tetranychidae)

Notulae ad Tetranychidas

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In previous publications I have already pointed to the fact that systematically and nomenclatorically there remains much work to be done in the genus *Bryobia*, and that the conception of a *Bryobia praetiosa* complex cannot be maintained in the way which is traditional. Other acarologists have also stated this fact and in the U.S.S.R. especially various new species have recently been described: i.e., by Reck, Bagdasarian and Wainstein. However, apart from these and other species that are well defined, there still exists the *praetiosa* complex that consists of a number of species that are difficult to separate.

Since I started the study of this genus I have come to the conviction that the *praetiosa* complex as it now exists must be divided into several groups of species. In many cases these groups can be defined rather well, but within each group the specific characters may be so complicated that great caution is necessary when describing new species. Much difficulty is caused by the great variability of these animals that may be exhibited even within one population.

It has recently been proved that within the *praetiosa* complex males may be present, as suggested by Dugès in Paris (1834). The first recent observation was by Mathys (1955). Also, my own material shows that in some species males are regularly present (though not in large numbers) whereas in other species they seem to be truly absent.

At present it is not yet possible to define all the groups of species of the genus *Bryobia*. For a number of groups, however, this is possible and I give the following key for their separation. This key applies only to adult females and attention should be paid to the fact that sometimes a tenent hair may be doubled, or split into 2 hairs. Larvae and nymphs have not the same number of tenent hairs as adults.

1a. Cephalic projections very short or lacking, empodia I with 2 tenent hairs . . . . . . *drummondi* group

b. Cephalic projections short, empodia I with rows of tenent hairs . . . . . . *sarothamni* group

c. Cephalic projections well developed . . . . . . *praetiosa* complex . . . 2

2a. Femora I with some strikingly long, stiff hairs (*speciosa* Berl. non Koch) . . . . . . *berlesei* group

b. Femora I with normal hairs 3

3a. Empodia I with 2 tenent hairs 4

b. Empodia I with more than 2 tenent hairs 5

4a. Outer cephalic projections slender with narrow bases . . . . . . *rubrioculus* group

b. Outer cephalic projections with broad bases, almost triangular . . . . . . *praetiosa* group

5a. Empodia I with 4 tenent hairs . . . . . . *speciosa* group

b. Empodia I with 8 or more tenent hairs . . . . . . *borealis* group

In some cases the morphological differences between the groups are so striking that perhaps later a division in subgenera will be justified.

The following additional remarks, which in some respects deviate from those expressed by Pritchard and Baker in their great standard work, concern the groups of the *praetiosa* complex.

borealis group:—To the extent that the descriptions permit one to judge, these mites are characterized by having relatively short legs I, genu I with only one ring of hairs, and empodia of tarsi I with 2 rows of tenent hairs. The species seem to prefer cool regions. This group includes *B. borealis* Oudms. 1930 from Spitzbergen (Svalbard), *B. glacialis* Berl. 1913 from Italian glaciers, and *B. serrata* (Cambr. 1876) from Kerguelen's Land. Males are unknown.

B. cristata Pritchard and Baker 1955 (non Dugès 1834) from Japan also has empodia I as above, but it seems to me that it does not belong to this group. I have not yet sufficiently studied this species and it frequently has males.

berlesei group:—This is based on *B. berlesei* v. Eyndh. 1957 (=*B. speciosa* Berl. 1888 (non C. L. Koch 1838)) and is characterized by the noticeably long and stiff hairs on femur I. This group seems to consist of small species that live in Central and Southern Europe. I have renamed Berlese's species.

speciosa group:—These mites have various striking characters of which the most important are the cephalic projections and the claws of legs II to IV. The tibiae I are more slender than genu I and tarsus I, many hairs of tarsus I project at a 90° angle, the hairs of the posterior margin are flabellate, and legs II are relatively short and in mounted specimens do not, or hardly, reach genu I. They live on grass and herbs and deposit their eggs there. Unlike some other species of the *praetiosa* group, these do not require hiding places.

I collected *Bryobia speciosa* from the original locality of C. L. Koch in the Tschifflicker Wald near Zweibrücken, Germany. A publication is in press.

As far as I can determine, the first author after Koch who described a mite of this group was Wainstein (1956) in the U.S.S.R., who gave it the name *Bryobia recki*. Males are unknown.

rubrioculus group:—This is composed of rather small species that live on fruit trees and related Rosaceae. They are characterized by having slender exterior cephalic projections with narrow bases that are separated by a deep incision from the interior ones, and by having flabellate hairs on the posterior margin. This group is based on the species *Sannio rubrioculus* Scheuten 1857. Scheuten gave a description and a primitive but distinct, coloured plate. I have collected mites with the red and green colours described by Scheuten in the original locality (Western Germany) where Scheuten was active. Males are unknown.

praetiosa group:—These mites have exterior cephalic projections with broad bases and nearly triangular, the incision between the exterior and the interior projections is wide and not very deep. The hairs of the posterior margin are spatulate, and the legs I are relatively more robust than those of *B. rubrioculus*. I collected *B. praetiosa* C. L. Koch 1836 at the original locality (Bösnergarten, Regensburg). To this group also belongs the original *B. cristata* Dugès 1834, which is still common in the public parks of Paris, France, and *B. kissophila* v. Eyndh. 1955, and probably also *B. ribis* Thomas 1894 from gooseberry. For the latter species the difficulty is that there are two forms on gooseberry, a larger and a smaller one.

The original *B. praetiosa* and *B. cristata* are closely related, but their biology is quite different. *B. praetiosa* lays winter eggs in which the embryo is present long before the moment of hatching and which attain a characteristic pink colour. I never found such eggs with *B. cristata*. The latter species, however, regularly produces males, as observed by Dugès, which I have not found with *B. praetiosa*. Both species always live in the neighbourhood of trees, stones, or houses, where they hide and deposit their eggs. They feed on grass and herbs. Together with related species they invade human dwellings. *B. kissophila*, however, never causes invasions though it often lives against the wall of houses, and also this behaviour has not been recorded with other groups.

REFERENCES

Berlese, A. 1888. Acari, Myriopoda et Scorpiones hucusque in Italia reperta, fasc. 51, pl. 1.

Dugès, Ant. 1834. Recherches sur l'ordre des Acariens en général et la famille des Trombidiés en particulier. Premier mémoire. *Ann. Sci. nat.*, ser. 2, 1: 15, 28–29.

Eyndhoven, G. L. van. 1955. *Bryobia* from Hedera, apple and pear (Acar., Tetran.). Notulae ad Tetranychidas 1. *Ent. Bericht.* 15: 340–347, f. 1–6.

Eyndhoven, G. L. van. 1956. *Bryobia cristata* (Dugès 1834) and *Bryobia rubrioculus* (Scheuten 1857) (Acar.). (Notulae ad Tetranychidas 3). *Ent. Bericht.* 16: 45–46.

Eyndhoven, G. L. van. 1957. L'interprétation de Bryobia speciosa Berl. (non Koch). Notulae ad Tetranychidas 4. *Ent. Bericht.* 17: 43–44.

Koch, C. L. 1836. Deutschlands Crustaceen, Myriapoden und Arachniden, fasc. 1, pl. 8.

Koch, C. L. 1838. Op. cit., fasc. 17, pl. 10.

Mathys, G. 1955. Les problèmes du bryobe précieux (*Bryobia praetiosa* Koch) dans le cadre de la lutte contre les araignées rouges. *Rev. romand. Agric.* II: 93-95 f. 1–4. (also in Publ. 492, XII. 1955, *Stations féder. d'essais agric.*, Lausanne).

Oudemans, A. C. 1930. *In*: Sig Thor, Beiträge zur Kenntnis der Invertebraten Fauna von Svalbard. *Skrift. om Svalbard*, fasc. 27: 102–103, pl. 16a.

Pritchard, A. E., and E. W. Baker. 1955. A revision of the spider mite Family Tetranychidae. *Mem. Ser., Pacif. Coast Ent. Soc.* 2.

Scheuten, A. 1857. Einiges über Milben. *Arch. Naturg.* 23: 104–112, pl. VII, f. 12–14.

Wainstein, B. A. 1956. On the fauna of the tetranychoid mites in the southern Kazakhstan. *Zool Jour.*, U.S.S.R. 35: 384–391, f. 1–6. (In Russian).

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